



GLOBAL CHANGE

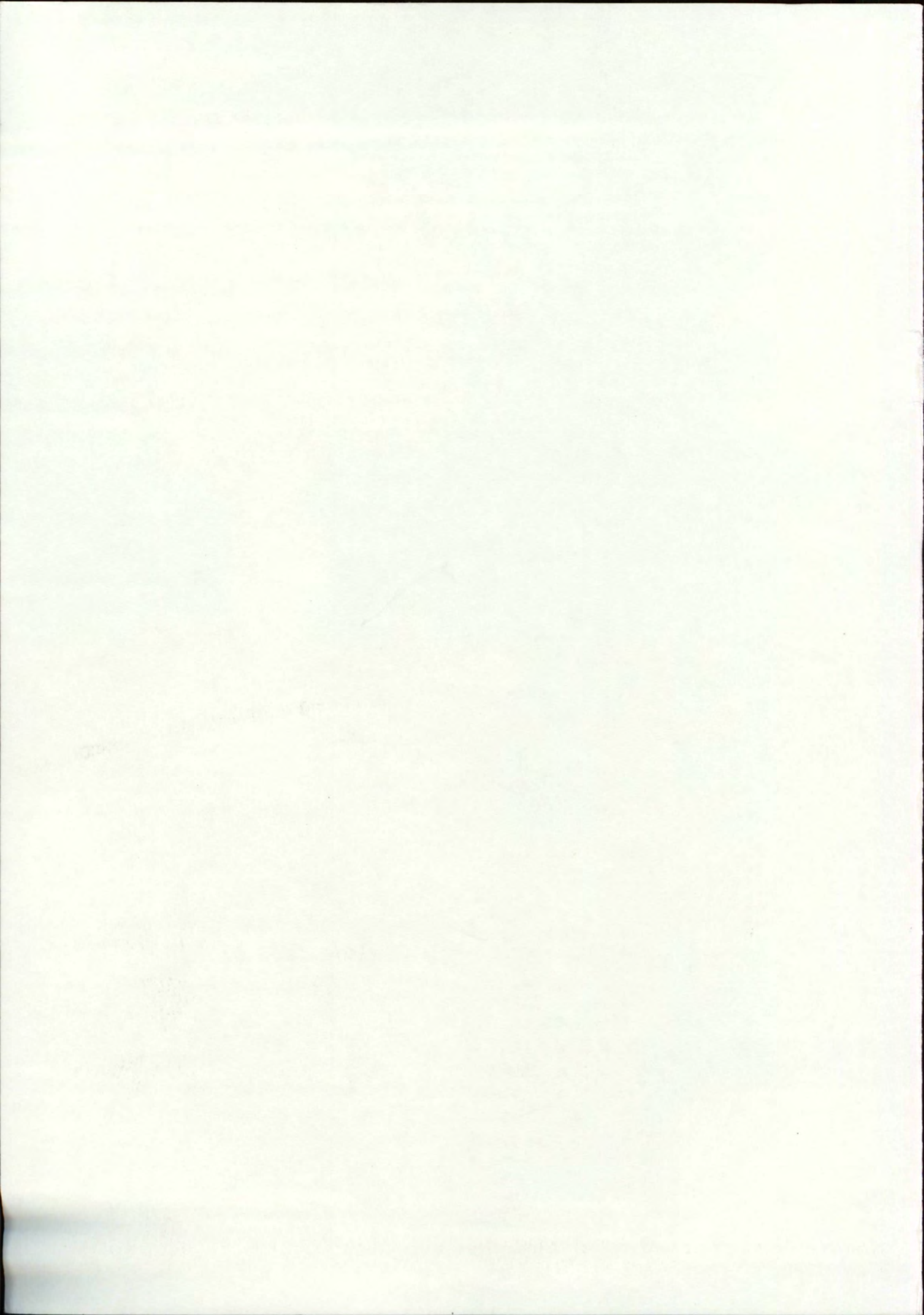
Dutch National Research Programme on Global Air
Pollution and Climate Change

**Modelling the impact of climate change
on the Wadden Sea ecosystems**

Rijkswaterstaat
Rijksinstituut voor Kust en Zee/RIKZ
Bibliotheek (Den Haag)

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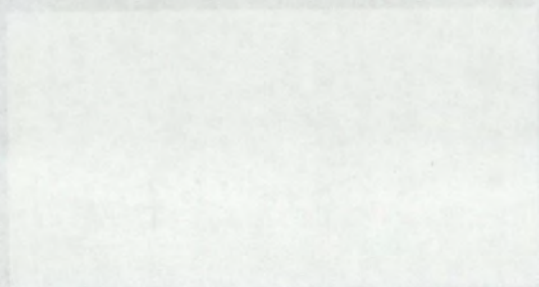
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Nationaal Onderzoek Programma Mondiale Luchtverontreiniging en Klimaatverandering (NOP)

Het Nationaal Onderzoek Programma Mondiale Luchtverontreiniging en Klimaatverandering (NOP) bevindt zich thans in de twee fase (1995-2001). De eerste fase, waarin 150 projecten zijn uitgevoerd, liep van 1990 tot 1995. Naar verwachting zullen in de tweede fase uiteindelijk circa 80 projecten worden uitgevoerd. Gezien de aard van het klimaatprobleem is een multi-disciplinaire benadering binnen het NOP noodzakelijk. Het programma is onderverdeeld in vier thema's:

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- II Kwetsbaarheid van natuurlijke en maatschappelijke systemen voor klimaatverandering
- III Maatschappelijke oorzaken en oplossingen
- IV Integratie en assessment

Het primaire doel van het NOP, als strategisch en lange termijn onderzoekprogramma, is te voorzien in de behoefte aan beleidsrelevante informatie voor de ontwikkeling van het nationale en internationale klimaatbeleid. Naast het bereiken van dit inhoudelijke doel, wordt er ook veel belang aan gehecht dat het onderzoek op de langere termijn verankerd zal blijven in de Nederlandse onderzoeksstructuur.

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National Research Programme on Global Air Pollution and Climate Change (NRP)

The National Research Programme on Global Air Pollution and Climate Change (NRP) is currently in its second phase, 1995-2001. The first phase, in which 150 projects were carried out, ran from 1990 to 1995. About 80 projects are expected to be finally realised in the second phase. The nature of the climate problem warrants a multi-disciplinary approach within the NRP. The programme is categorised into four themes:

- I Dynamics of the climate system and its component parts
- II Vulnerability of natural and societal systems to climate change
- III Societal causes and solutions
- IV Integration and assessment

The primary objective of the NRP as a strategic and long-term research programme is to meet the demand for policy-relevant information for the development of national and international climate policy. Besides realising this substantive objective, a great deal of importance is attached to the long-term anchoring of the research within the Dutch research structure.

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For chapters 4, 6 and 7, C.J. Smit (Alterra Texel) was responsible as editor.

ABSTRACT

In the framework of the Dutch National Research Programme on Global Air Pollution and Climate Change, ecological responses of the Wadden Sea ecosystem to changing climate conditions have been studied. A number of characteristic processes, organisms and steering factors have been chosen as themes.

From morphological studies it followed that a future increase in storm surge level and frequency will seriously affect salt marsh development; Friesian salt marshes will develop less fast; salt marshes at the Groninger main land will erode.

Loss of foraging possibilities for migrating birds is the main cause of a decline in bird numbers as a result of sea level rise.

Higher environmental temperatures may cause a lower larvae growth development for the Baltic Tellin *Macoma balthica*. From a comparison of southern and northern populations it followed that southern populations are possibly better adapted to higher temperatures, and they might have a chance to move northwards when situations change.

From the mesocosm studies it followed that for bivalves, the two major climate change aspects had opposite effects: sea level rise stimulated biomass and production, whereas temperature rise depressed bivalve production.

A developed expert system (EcoFuzz) covers time scales that exceed the ones feasible for laboratory research or experiments in model systems or the field. It provides a suitable means for the incorporation of ambiguities and lack of quantitative data into a classification scheme.

The description for benthic filter feeders in the integrating ecosystem model EcoWasp was capable to reproduce and laboratory filtration and respiration measurements, individual mussels growth rates in the field and mussel bed grazing intensities upon algae and particulate matter. Primary production remained underestimated by the model.

Scenario studies showed that the Wadden Sea system is especially sensitive to sea level changes, and temperature changes, especially to whole year temperature changes.

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SUMMARY

In the framework of the Dutch National Research Programme on Global Air Pollution and Climate Change, we investigated the ecological response of the Wadden Sea ecosystem to changing climate conditions.

The project "Modelling the impact of climate change on the Wadden Sea ecosystem" matches the targets mentioned in Theme II of the climate change programme of the Dutch Government "Vulnerability of natural and societal systems to climate change". In this theme II, the study results are expected to show us how natural systems react upon climate change phenomena, and therefore: knowledge of the overall-impact is needed. Furthermore, the consequences for the sustainable use of such coastal areas are mentioned as target of theme II.

We focused on a number of characteristics: morphological phenomena, shell fish processes and birds. We applied three different integrating methods: integration by a model ecosystem study, by the setup of an expert system, and by the further development and application of a dynamic ecosystem model.

We also choose a number of key steering factors to focus on: temperature rise, water level rise and changing tidal volume, increasing strengths of wind and storms, and increasing fresh water inflow as a results of an increasing precipitation in the more central sites of Europe.

The study on morphological processes in the salt marsh area and the tidal flats in front of these areas showed that local wave action determines whether the supplied sediment stays in suspension or is deposited within the sedimentation fields of the salt marshes. The height and maintenance of the brushwood groynes determines the wave action during calm weather condition. During storm surges, when the groynes are submerged, currents are still interrupted but the wave dampening effect is reduced significantly.

A future increase in storm surge level and frequency will seriously affect salt marsh development. Salt marsh areas of the mainland coast of the Dutch Wadden Sea need a two-year period to recover from a year with many storm surges. At the moment, the salt marshes along the

coast of Friesland attain a positive accretion budget, so the effect of an increase in storm surges will lead to a decrease in accretion. The salt marshes along the coast of Groningen show growth stagnation; an increase in storm surges will directly lead to erosion in this area.

The study on bird migration focused on the improvement of bird models. Dynamic models as DEplete and LARGEPOP are applicable to investigate climate change effects in a foraging area (DEplete) or on a world wide scale (LARGEPOP). Analysis with DEplete, and with the habitat suitability model HABITAT both predict a decline of bird numbers in the Wadden Sea as a result of sea level rise. Loss of foraging possibilities is the main cause of such a decline. Because also conditions in breeding areas are affected, an overall view is needed; LARGEPOP predicts a world wide decline of the Brent geese population as a result of sea level rise and changing conditions during the breeding season.

Higher environmental temperatures may cause a lower Body and Gonadal Mass Index, and a lower larvae growth development for the Baltic Tellin *Macoma balthica*. This is demonstrated by the research on shell fish development and reproduction. We compared *M. balthica* from the Gironde, at the southern border of the distribution with populations living further north. Development of larvae from the Gironde are not affected at high temperatures like the Balsfjord (Norway) larvae are. The results indicate that European population(s) of *Macoma balthica* will for sure be affected by higher temperatures. Populations now living further south are possibly better adapted to higher temperatures. Considering the dispersal abilities of *Macoma balthica* these populations might have a chance to move northwards when situations change.

The two aspects of climate change studied in the mesocosms, sea level rise and temperature rise, have an impact on the tidal flat macrobenthos community. In neither of the experiments the numbers of the organisms were affected by the treatment, not by the temperature rise, nor by a sea level rise. It seems that in situations with an increased water level, larvae settlement and growth was more successful. Also, in the high level situation, growth of adults turned out to be better. The length of the inundation period and the biomass production showed a proportional relationship.

With an increased temperature, individual biomass of cockles was lower than in the normal situations. These deviations did not occur during a winter period, but in the April-May period. The model systems were dominated by *Arenicola marina* (especially juveniles), that did not show any relationship with temperature. Therefore, an overall biomass density response to changing temperatures was not found.

For bivalves, the two major climate change aspects had opposite effects: sea level rise stimulated biomass and production, whereas temperature rise depressed bivalve production.

A long term effect cannot be deduced from these experiments, since recruitment did not take place in the basins.

An attempt to integrate climate change related phenomena has been done by the development of an expert system. Such a tool also covers time scales that exceed the ones feasible for laboratory research or experiments in model systems or the field. In this expert system (EcoFuzz), experimental observations, model results and expert knowledge can be integrated and the results can be presented in both a qualitative and a quantitative way. Furthermore, the model offers the user the possibility to define and evaluate cases. In order to develop a model for the whole ecosystem of the Wadden Sea a modular, incremental approach was chosen, as was the application of fuzzy set theory. It provides a suitable means for the incorporation of ambiguities and lack of quantitative data into a classification scheme.

The functionality of EcoFuzz includes the definition of fuzzy membership functions for all relevant aspects, the definition of fuzzy inference rules, and the evaluation of scenarios in a graphical form. The input of this expert system consists of observations from mesocosm experiments, results of model computations, and expert knowledge.

The integrating ecosystem model EcoWasp has been improved considerably during the project, although some of the targets were not realized. Especially the activity description for benthic filter feeders turned out to be capable to describe and laboratory filtration and respiration measurements, individual mussels growth rates in the field and mussel bed grazing intensities upon algae and particulate matter. Thus the model integrated experimental data from completely different time and size scales. The effect of bird predation, however, was not directly

implemented in the model, and needed to be part of a general mortality term.

The computations simulated benthic filter feeder biomass quite well; primary production remained lower than figures resulting from extrapolations from field experiments. Until now it has not been possible to compute together a good fit for chlorophyll-a (algae), and for benthic filter feeder biomass and primary production and benthic filter feeder growth and filtration activities. Only primary production remained underestimated by the model.

Effects of climate change have been estimated. The system seems to be sensitive to sea level changes, and temperature changes, especially to whole year temperature changes. With increasing winter temperatures, especially the tidal flat filter feeders lost biomass densities, probably because their individual budget is more under stress than sub-tidal mussels because of the tidal effects.

The main picture resulting from the simulations is that the results are sensitive for timing aspects. Changing periods of development for algae and filter feeders cause large effects; as a result from different conditions for mussel larvae to feed to survive. Changing predation pressure caused by a different behaviour of e.g. crabs and shrimps are still left out of the model; these probably will amplify such timing effects.

SAMENVATTING

In het kader van het Nationaal Onderzoeksprogramma Mondiale Luchtverontreiniging en Klimaatverandering is onderzoek verricht naar de responsie van het Waddenzee ecosysteem op klimatologische veranderingen.

De studie "Modelling the impact of climate change on the Wadden Sea ecosystem" past binnen de doelen die gesteld zijn in Thema II van het van het klimaat-programma van de Nederlandse Overheid "Kwetsbaarheid van natuurlijke en maatschappelijke systemen voor klimaatverandering". Verwacht is dat de resultaten die binnen dit thema II bereikt worden ons zullen leren hoe natuurlijke systemen reageren op verschijnselen die aan klimaat-veranderingen gekoppeld zijn. Geïntegreerde kennis van de gevolgen is een vereiste.

Ook is als doelstelling genoemd van Thema II dat de gevolgen voor het verantwoord gebruik van kustsystemen beter bekend worden.

Binnen ons onderzoek hebben wij ons beperkt tot een aantal karakteristieke processen. Wij hebben aandacht besteed aan enkele morfologische aspecten en aan de gevolgen voor schelpdieren en vogels. Effecten op het systeem als geheel zijn beschreven met een drietal integrerende methoden: een integraal dynamisch ecosysteemmodel, een expert systeem en een studie in een modelecosysteem, waar met metingen een systeemrespons kon worden gevolgd.

Eveneens hebben wij ons op een aantal sleutelfactoren gericht: temperatuurverandering, zeespiegelstijging en een veranderend getijdenvolume, toenemende sterktes van wind en stormen, en een toenemende instroom van zoet water als gevolg van toegenomen neerslag in de meer centraal-Europese gebieden.

De studie naar morfologische processen aan de kwelders en de platen vóór deze gebieden gaf aan dat lokale golfwerking bepaalt of fijn materiaal in suspensie blijft dan wel sedimenteert in de sedimentatiegebieden van de kwelders. De hoogte en de staat van onderhoud van de rijstdammen bepalen de golfwerking gedurende kalm weer. Tijdens stormvloed, als de rijsthouten dammen onder water staan, worden de golven nog wel onderbroken, maar het dempende effect

van de dammen is dan aanzienlijk geringer.

Als in de toekomst de hoogte van het water tijdens stormen toeneemt, en de frequentie van overvloedingen eveneens, zal de ontwikkeling van kwelders ernstig negatief beïnvloed worden. De vastelandskwelders in de Nederlandse Waddenzee hebben een periode van twee jaar nodig om te herstellen van een jaar met veel stormvloeden. Momenteel is het sedimentbudget van de kwelders langs de Friese kust nog positief; een toename van stormvloeden zal een verminderde opslibbing te zien geven. De opslibbing op de kwelders langs de Groningse kust is al vrijwel nul; een toename van stormvloeden zal een erosie van de kwelders aldaar inhouden.

De studie naar migratiepatronen van vogels heeft zich geconcentreerd op de verbetering van beschrijvende modellen. Dynamische modellen als DEplete en LARGEPOP zijn toepasbaar om effecten in een foerageergebied (DEplete) te onderzoeken, of effecten op een wereldwijde schaal te analyseren (LARGEPOP). Een analyse met DEplete, alsook die met het habitatgeschiktheidsmodel HABITAT, voorspelt een afname van het aantal vogels in de Waddenzee wanneer de zeespiegel stijgt. Het verlies aan foerageergebied is de hoofdoorzaak van zo'n achteruitgang.

Omdat ook de omstandigheden in de broedgebieden worden beïnvloed is een integrale benadering gewenst. LARGEPOP voorspelt een wereldwijde afname van de populatie brandganzen als gevolg van zeespiegelstijging en gewijzigde condities gedurende het broedseizoen.

Hogere omgevingstemperaturen kunnen de oorzaak zijn dat nonnetjes *Macoma balthica* aan het einde van de winter een lager conditie-index hebben, en een lagere gonadenmassa-index. Hierdoor kan na hogere wintertemperaturen een slechtere reproductie en een slechtere ontwikkeling van larven optreden. Dit is aangetoond na onderzoek naar de ontwikkeling en reproductie van deze schelpdieren. We hebben *M. balthica* uit de Gironde, het meest zuidelijke deel van het verspreidingsgebied van de soort, vergeleken met populaties die noordelijker aangetroffen worden. De ontwikkeling van larven uit de Gironde werd niet beïnvloed door hogere temperaturen, in tegenstelling tot die van larven uit de Balsfjord (Noorwegen). Deze resultaten tonen aan dat Europese populaties zeker beïnvloed zullen worden door hogere temperaturen.

Zuidelijke populaties zijn mogelijk beter aangepast aan hogere temperaturen. Gezien de mogelijkheden tot verspreiding van *M. balthica* hebben deze zuidelijke populaties kansen zich naar noordelijker streken te verplaatsen wanneer de omstandigheden zich wijzigen.

Zowel zeespiegelstijging als temperatuurveranderingen hebben invloed op de macrobenthos-gemeenschap van getijdenplaten; beide aspecten zijn onderzocht in middelgrote modelecosystemen: mesocosms. De aantallen organismen werden niet, in geen van beide gevallen, beïnvloed. Vestiging en groei van larven bleek succesvoller te verlopen bij een hoger waterniveau, evenals de groei van grotere exemplaren. De lengte van de inundatieperiode en de biomassaproductie bleken evenredig gerelateerd. Met een stijgende temperatuur bleek de individuele biomassa van kokkels lager te zijn dan in de normale situatie. Dit verschil ontstond niet in de winter periode, maar in de periode maart-april. De modelsystemen werden gedomineerd door *Arenicola marina*, in het bijzonder door juvenielen, die geen verband met de temperatuur vertoonden. Daarom vertoonde de algehele biomassa geen significante respons op temperatuurveranderingen.

Op schelpdieren hadden de twee klimaataspecten tegengestelde effecten: zeespiegelstijging stimuleerde de biomassa en de productie, terwijl een temperatuurverhoging juist de productie van de schelpdieren remde.

Omdat in de bekkens geen reproductie plaats vind, wat een sleutelfactor is bij langere-termijnstudies, kon een effect op lange termijn kon niet uit de experimenten worden afgeleid.

Een poging om verschijnselen die met klimaatverandering van doen hebben te integreren is gerealiseerd door de ontwikkeling van een expertsysteem. Zo'n gereedschap kan ook tijdschalen bevatten die uitstijgen boven wat in het laboratorium, mesocosms of het veld mogelijk is. In dit expertsysteem (EcoFuzz) kunnen experimentele observaties, model resultaten en expertkennis geïntegreerd worden, en zowel kwalitatief als kwantitatief gepresenteerd worden. Verder biedt het model de mogelijkheid 'cases' te definiëren en te evalueren. Om een model voor de hele Waddenzee te ontwerpen werd gekozen voor een modulaire, incrementele benadering, en voor de implementatie van 'fuzzy set'-theorie. Dit biedt een geschikte mogelijkheid om dubbelzinnige aspecten in een classificatieschema onder te brengen; het ontbreken van kwantitatieve gegevens

hoeft eveneens daarbij geen bezwaar te zijn.

De functionaliteit van EcoFuzz omvat ook de definitie van 'fuzzy membership' functies voor alle relevante aspecten, de definitie van 'fuzzy' interferentieregels, en de grafische evaluatie van scenario's. Dit expertsysteem is gevoed met waarnemingen uit de mesocosm experimenten, resultaten van modelberekeningen en expertkennis.

Het integrerende ecosysteemmodel EcoWasp is gedurende het project aanzienlijk verbeterd, alhoewel een deel van de doelen niet gerealiseerd kon worden. In het bijzonder de beschrijving van de activiteit van bentische filtreerders bleek in staat te zijn én laboratorium waarnemingen aan filtratie en respiratie te beschrijven, én individuele groeisnelheden van mosselen in het veld, én begrazing van algen en ander particulier materiaal boven een mosselbank. Het model integreerde aldus experimentele data van totaal verschillende tijd- en grootteschalen. Het effect van predatie door vogels kon echter niet in het model geïmplementeerd worden, en moest nog via een algehele sterfteterm benaderd worden.

De modelberekeningen reproduceerden de biomassa aan bentische filtreerders redelijk goed; de primaire productie bleef lager dan de (literatuur-)waarden voor veldexperimenten. Tot nu toe bleek het niet mogelijk een goede overeenkomst voor zowel chlorofyll-a (algen), als bentische filtreerders, als voor filtratieactiviteiten tegelijk te verkrijgen. In de huidige berekeningen bleef vooral primaire productie achter bij de velddata.

Gevolgen van klimaatveranderingen zijn geschat. Het systeem blijkt gevoelig te zijn voor zeespiegelstijging, en voor temperatuurveranderingen, in het bijzonder wanneer die gedurende het hele jaar optreedt. Stijgt de wintertemperatuur, dan neemt vooral de filtreerderbiomassa op de platen af. Vermoedelijk staat hun individuele budget meer onder druk dan dat van de filtreerders in het subtidal.

Het algehele beeld dat uit de simulaties naar voren komt is dat de resultaten gevoelig zijn voor 'timing' aspecten. Verschuift de periode waarin algen gaan bloeien ten opzichte van het moment waarop filtreerders reproduceren, dan ontstaat een ander systeemgedrag. Andere karakteristieken zoals het voorkomen van krabben en garnalen zijn niet in het model meegenomen; maar deze zullen ongetwijfeld zo'n effect nog eens versterken.

1 PREVIEW

1.1 Framework and considered area

The present study deals with expected or possible climate change phenomena that may influence ecological characteristics or the ecological functioning of the Dutch Wadden Sea. The study matches the targets mentioned in Theme II of the climate change programme of the Dutch Government “Vulnerability of natural and social system to climate change”. In this theme II, the study results are expected to learn us how natural systems react on climate change phenomena: knowledge of the overall-impact is needed. Furthermore, the consequences for the sustainable use of such coastal areas is mentioned as target of theme II.

1.2 Expected effects of climate change

There are many different effects related to climate change; some of these will certainly affect the functioning or characteristics of the Wadden Sea ecosystem, and some possibly will not have any effect at all.

In our study, we are not looking for primary effects of climate change (like: *what the temperature change might be*), but moreover, we are studying effects of the some relevant phenomena, like: *what will be the effect of a certain temperature change*. What determined our choice, is a result of previous studies (see text box 1.1).

For example, we decided not to study effects of UV-radiation, or the effects of

The project focusses on quantifying risks from changing temperatures and water levels on the Wadden Sea ecosystem by integrated model computations. Further development and application of an integrated ecosystem model is the core of the project. Model improvement will result from studies on bird migration and food selection processes, on mesocosm integrated experiments and shell fish processes, on salt marsh accretion and exchange processes, and on morphological processes inside the basin and interrelations with benthic fauna development. All sub-projects involve (further) development of sub-models.

Text box 1.1 Aim of the project as described in the proposal

increased carbon dioxide contents upon primary production of the system. The choice not to study CO₂-effects is based upon the consideration that carbon dioxide in aquatic systems is

provided as dissolved CO₂, and this is assumed to be sufficiently available. Shortages are not expected under present conditions. UV-B radiation effects have been considered as subject, but was not chosen because a) we had to limit our number of themes and b) we realized that UV-B radiation will extinct within a few centimetres, and therefore, will have limited effect upon aquatic processes.

What may be affected as Wadden Sea characteristics is the ebb and flood regime, and its fluctuating morphology. Morphology is influenced by eroding forces due to water flows and waves and by natural deposition of sand and silt in more quiet regions, or by biologically mediated deposition. Temperature effects are expected to be important as well, because the system is shallow, and therefore it will react relatively fast to changing air temperature, solar radiation and changes in long-wave back-radiation. Due to changing precipitation, the inflow of fresh water, as well the nutrient content of this inflowing fresh water, may change and thus alter the nutrient supply of the coastal waters and influence primary and secondary production. Also, on a individual scale, temperature change and sea level rise may effect the functioning of single animals, or may allow other or better survival chances for allochthonous species. Last but not least, changing inundation times, food abundances or food availability may seriously effect populations of birds species migrating along the Eat-Atlantic flyways.

These aspects of climate change effects form the basics of our research project, and they will be paid attention to in this report.

1.3 Setup and organisation of the project

In the first stage of the project, two projects had to be merged. The one was proposed by the former Institute for Forestry and Nature Research (IBN, project leader Prof. Dr. W.J. Wolff), the other was proposed by the National Institute for Coastal Zone Management (RIKZ, project leader Dr. F. Colijn). Also, the financial size of the project had to be reduced substantially. Unfortunately most of the projects goals were reduced much less then the funding, a less favourable situation as the course of the project would show.

Nevertheless, a final product has been achieved, meeting most of the goals mentioned in the project proposal, although some of the targets could not be realised. And, the project result gives

us substantial information on Wadden Sea characteristics and their response to climate change phenomena.

During the project, the organisation has (also) been changed. First Dr. L.W.J. Higler took over the principal scientist position from Prof. Dr. W.J. Wolff (1-1-1996), on 1-1-1999 Dr. Ir. A.G. Brinkman became the third project leader in line.

1.4 Partnership

After the merging of both projects, the study group (Fig. 1.1) consisted of

- ALTERRA (before 1-1-2000: Institute for Forestry and Nature Research, IBN), covering three different theme's:

I-a Ecosystem modelling: Further model development for the impact of climate change on the Wadden Sea. This project, with project I-b, is assumed to be the integrating project for all the other activities.

II Bird migration processes and modelling: Aims at a further unravelling of the relationship between the foraging needs of migrating birds and the Wadden Sea system. The effects of sea level rise are expected to be the most important thread of the foraging capabilities of the system. Principal scientist Dr. B.J. Ens. Results have to be implemented into the ecosystem model, and as such part of I-a.

III-a Mesocosms research and modelling: Process research on effects of temperature and water level. Principal scientist Dr. K. Kersting. Also: testing of hypotheses, analysis by and calibration of the ecosystem model, and as such part of (I-a)

- Netherlands Institute for Sea Research (NIOZ).

III-b Mesocosms research and modelling: Laboratory and mesocosm research at species level. Principal scientist Dr. J. Beukema; drs. J. Drent did most of the job as PhD-fellow. III-a and III-b worked closely together as far as the subject dealt with mesocosm work. Results are meant to be implemented into I.

- National Institute for Coastal Zone Management (RIKZ).

I-b Integrating climate change effects by the development and application of a fuzzy

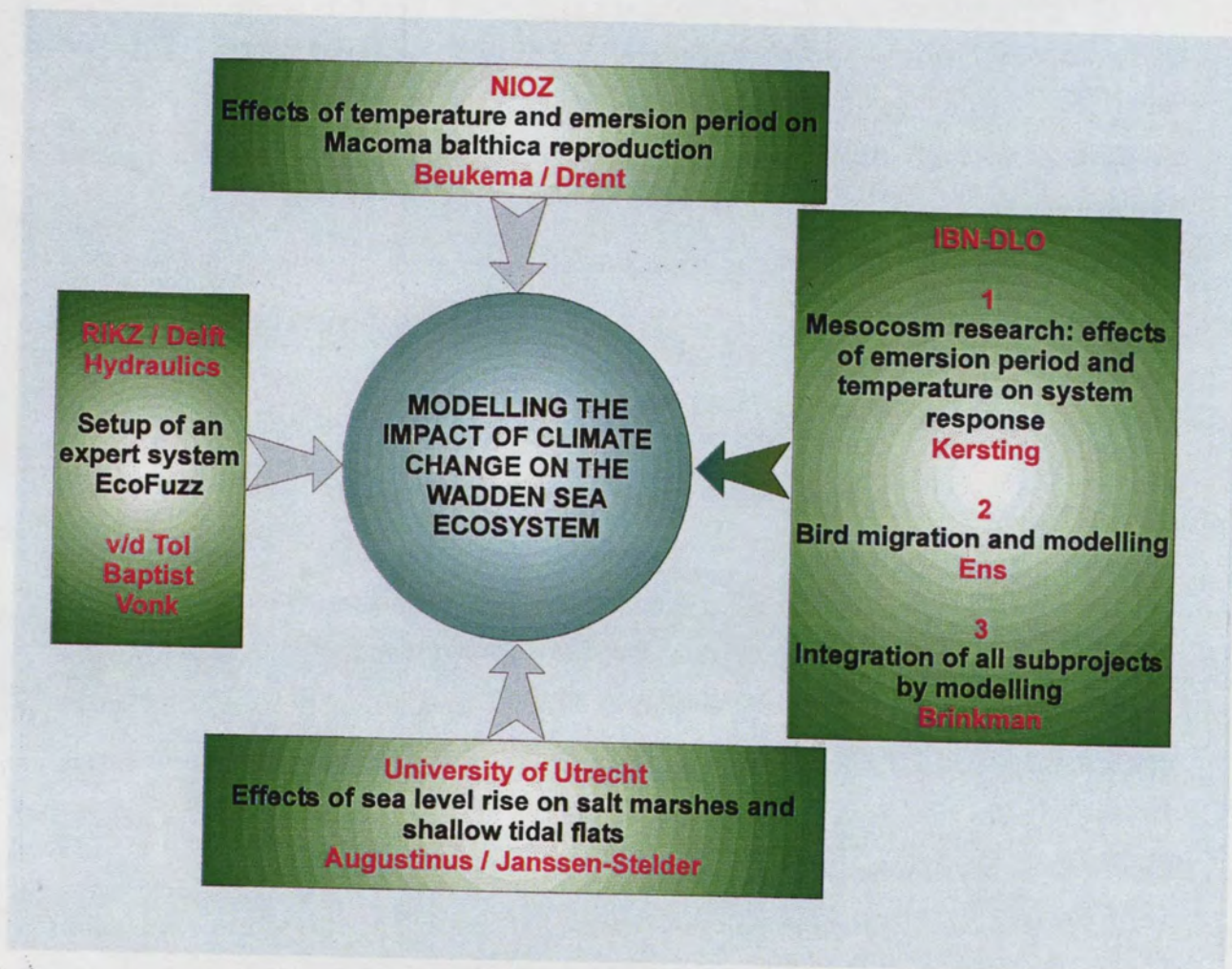


Fig 1.1 The project cooperation

model. Principal scientist Drs. M. van der Tol; Delft Hydraulics, with Ir. M. Baptist and Dr. M. Vonk, performed the job.

- University of Utrecht (RUU), department of Physical Geography

IV Saltmarsh and tidal flat processes, research and modelling. Development and stability of salt marshes and the tidal flats in front of these areas. Principal scientist Dr. P. Augustinus, drs. B.J. Janssen-Stelder did most of the job as PhD-fellow. The aim, to couple results with the ecosystem model (I-a) turned out to be a too optimistic one. This part of the project could not be realized.

Thus, the project knows two integrating projects (I-a and I-b), the first one based upon a dynamical model description, the second aiming at the development of a knowledge-base system, where more qualitative descriptions play a major role.

Twice a year the researchers met during a day, to inform each other on their progress and their setbacks.

To back-up the scientific process as well as the usefulness of the work, an audit group was formed, consisting of:

Ing P. Feddema	Wadden Advies Raad, Leeuwarden
Prof. dr. ir. J. Grasman	Wageningen University, Mathematics Group, Wageningen
Dr. R.H.G. Jongman	Wageningen University, Dept Environmental Sciences, Land Use Planning Group, Wageningen
Ir. J.G. de Ronde	RIKZ (National Institute for Coastal Zone Management), Den Haag

1.5 Application of results to other areas

We restricted our study to the Dutch Wadden Sea area, but the study has been set up in such a way that results may very well be applicable to other comparable tidal areas.

2 OVERVIEW OF CLIMATE CHANGE SCENARIO'S

2.1 Introduction

In the present project, we are dealing with a number of forcing functions, representing expected, or possible effects of global climate change. Most of the effects deal with changes in averages or seasonal variations of temperature, wind speeds, precipitation and sea level. In this chapter 2, a brief outline of relevant scenario's is presented.

2.2 Sources

A huge number institutions deliver results on climate change, based upon expected or assumed forcing functions. These forces concern possible developments of social structures, land and energy uses, and many more. Many of these basic assumptions, as are the results, are distributed by the IPCC, the Intergovernmental Panel on Climate Change, jointly established by the United Nations Environment Programme (UNEP) and the World Meteorological Organisation (WMO). IPCC partly acts as a coordinator and distributor of scenario's on climate change, as well on the cause side, as on the effect-side. Some of the last ones, being important for our study, will be outlined below.

For our study, scenario's provided by the Hadley Centre are most applicable. The NRP-II Programme Office in Bilthoven provided us with these results (Verweij & Viner, 2001). Based on the IPCC-scenarios, the Royal Netherlands Meteorological Institute KNMI (Können et al, 1997) estimated future changes for the local situation in the Netherlands.

2.3 Present developments

As shortly mentioned above, we restrict ourselves to a number of phenomena. Changes in

- temperature
- average sea level
- maximum, minimum levels

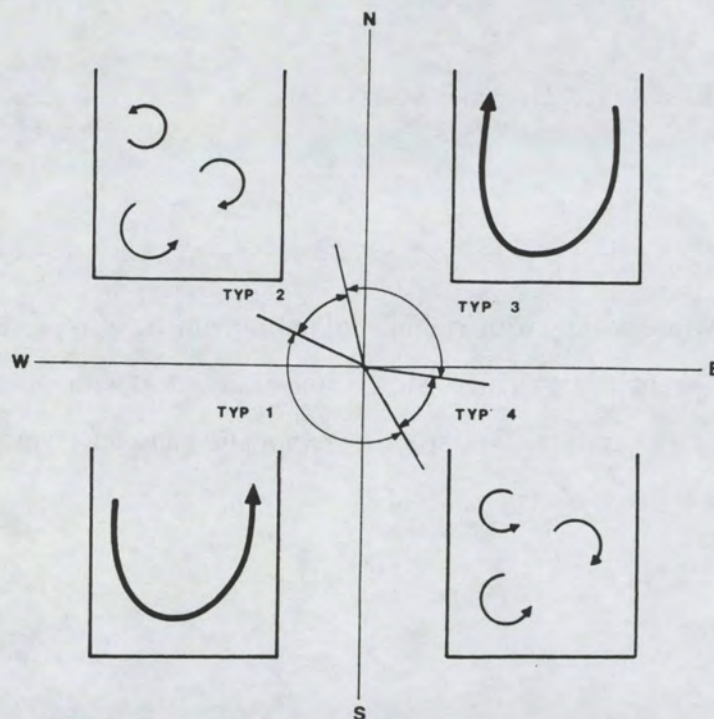


Abb. 1. Schematische Zirkulationsmuster der Nordsee unter Windeinwirkung aus den angegebenen Richtungssektoren; Typ 1: Grundmuster.

Fig. 2.1 Schematic representation of changing water circulation patterns in the North Sea, as affected by a change of the dominant wind directions. From (Backhaus, 1993).

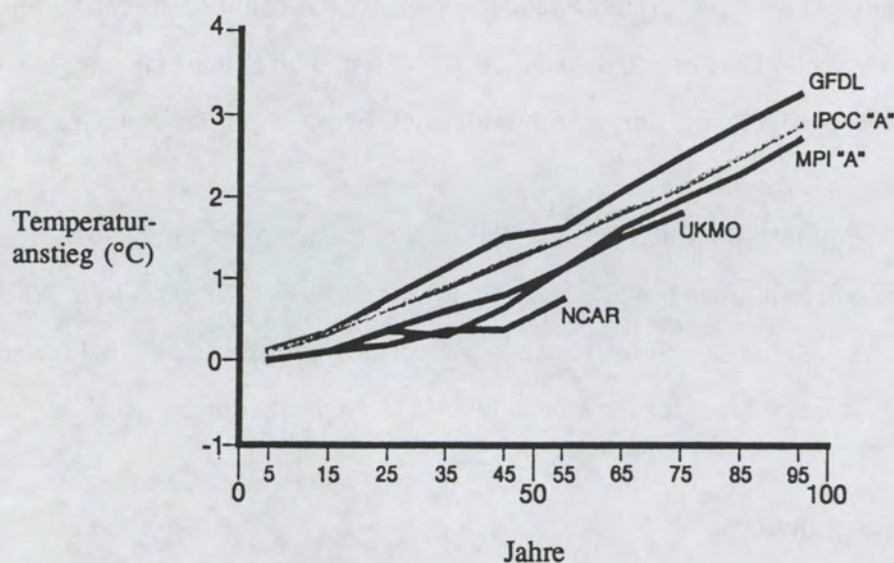


Abb. 1. Berechneter zeitabhängiger mittlerer Temperaturanstieg an der Erdoberfläche nach mehreren gekoppelten Ozean-Atmosphäre-Modellen sowie für maximal zwei Szenarien (A = business as usual, D = drakonische Maßnahmen). GFDL = Geophysical Fluid Dynamics Laboratory, Princeton; NCAR = National Center for Atmospheric Research Boulder, UKMO = United Kingdom Meteorological Office, Bracknell; MPI = Max-Planck-Institut für Meteorologie.

Fig. 2.2 Temperature rise scenarios for the coming century. Taken from Graßl (1993).

- average wind speed
- storm frequency

have been taken into account. Other possibilities like wind direction have not been considered at all, but one. Backhaus (1993) explains that it very well may affect the North Sea circulation pattern (Fig.2.1). If such a change occurs, the situation in the North Sea regions close to the Wadden Sea may change drastically, since the dominant water source will be a one very different from the present situation. Fish distribution and larvae transports will definitely differ completely from the present situation. Because also nutrient sources for the Wadden Sea will change, the eutrophication state for most of the areas will change as well.

2.4 Scenario's

2.4.1 Temperature

As an example, we took Fig. 2.2 from Schnellhuber and Sterr (chapter 2, by H. Grassl). It represents an expected temperature change at the earth' surface, but it does not represent the accompanying changes in water temperature. Also, since we expected that effects of small changes would be hard to measure, we considered a drastic change of 4 degrees Celsius water temperature increase. Based on IPCC scenario's (see eg. IPCC 2000), the KNMI mentions an increase of 1-2 °C in 2050 with a maximum of 4 °C in 2100 for the Dutch situation. Temperature rise in winter is expected to be higher than in summer.

2.4.2 Average sea level

Data for the Dutch coastal area (eg. Bouwmeester, 1993, Fig. 2.3) show an average increase of the mean tidal level of about 18 cm y⁻¹. This value is regarded as the 'present rate' of sea level rise. Increased rates, as forecasted by several studies range from almost 36 cm cm y⁻¹ as 'most likely' rates for the local situation, to 60 cm y⁻¹ as 'high rates'. A worst case scenario value reads 100 cm y⁻¹.

The Hadley Centre provided us with an average expected rise as presented in Fig 2.4, which has

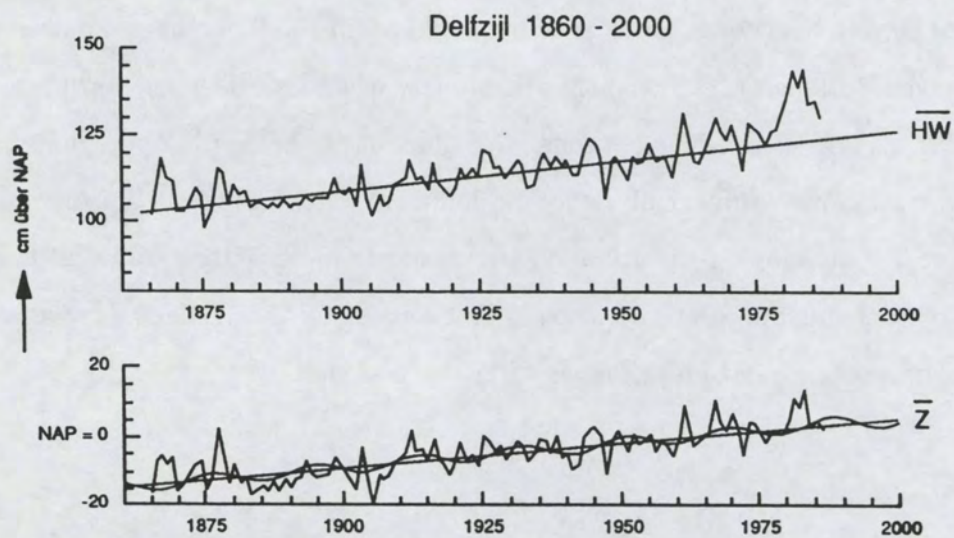


Abb. 4. Mittleres Hochwasser (HW), mittlerer Meeresspiegel (Z), mittleres Niedrigwasser (NW) und mittlerer Tidenhub (TH) bei Delfzijl.

Fig. 2.3. Observed sea water level at the Dutch coast. Taken from Bouwmeester (1993)

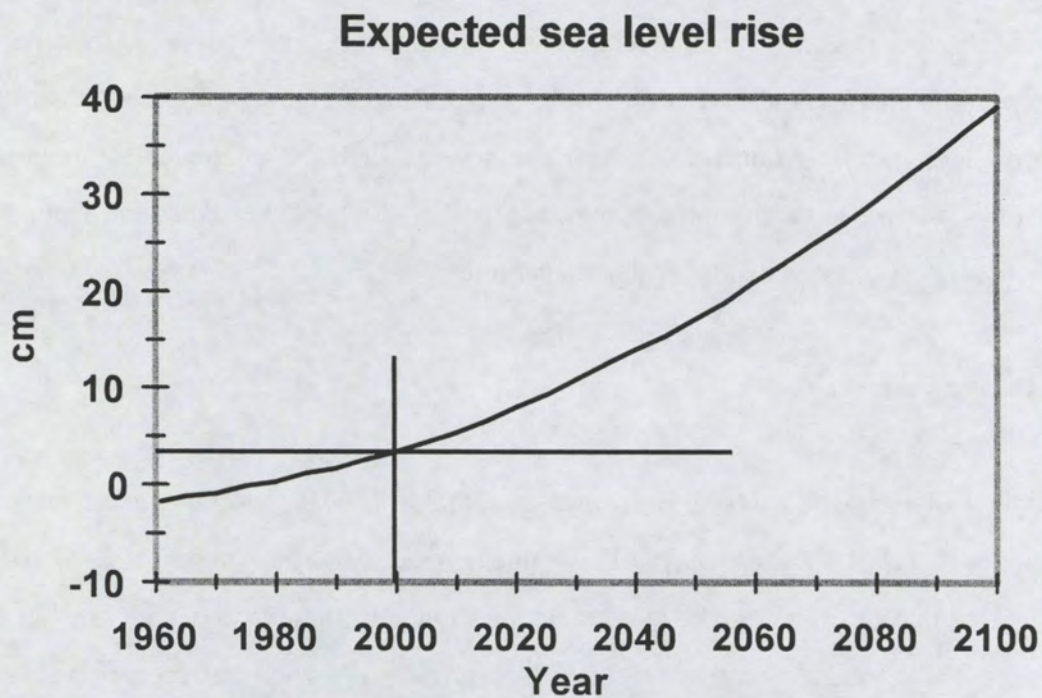


Fig. 2.4. Expected sea level rise, provided by the Hadley Centre

been the basis for our study. According to Bouwmeester, the mean high water level increased somewhat faster than the mean levels during the last century. For the future this would imply that the local tidal amplitude is also expected to increase. As a result, the tidal volume (the amount of water entering and leaving a tidal area each tide) will increase. A 5 cm increase equals about 5% of the present tidal range value. Although the tidal volume is not a linear function of the range, a 5% increase of this tidal volume can be seen as a first estimate of the changes to be expected.

2.4.4 Average wind speed

Data series are available for the period 1970-1999 (the present situation) and 2060-2090 (the expected situation). In Fig.2.5 an example is shown; wind speed is expected to increase somewhat during certain months, but the picture is not very clear.

2.4.5 Storm frequency

One of the expected aspects of climate change is that not only average wind speeds will increase, but also the frequency and intensity of extremes, ie, storms. No clear data are provided by Hadley. Top 10% -wind speeds are about 1.5* as high as average values, as are the maximum values when not daily but 6-hourly values are considered. The shorter the averaging period, the larger the differences. Maximum wind speeds mentioned in reports are usually 10 minute-averages; for storm surges also duration is relevant. Since water bodies need some time to react on changes in wind conditions, 10 minute wind averages are not considered as relevant for the intensity of waves. According to KNMI (Können et al, 1997), there is a chance to have more and heavier storms, but this expectation is highly uncertain.

2.4.6 Solar radiation

Data series are available as averages for the period 2089-2099. For a comparison with present radiation intensities, De Kooij-data from KNMI (KNMI 1976 - 1995) have been used. Data are

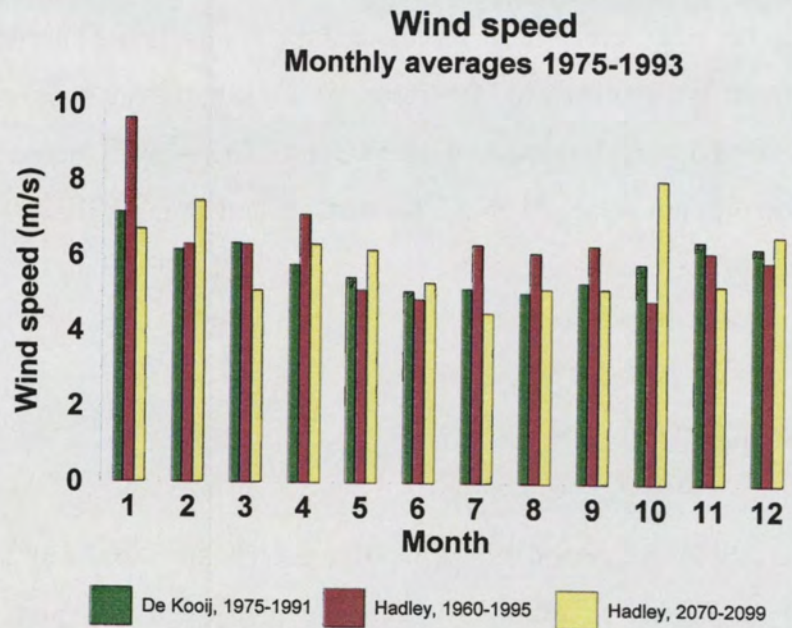


Fig. 2.5 Present and expected future wind speeds for the Wadden Sea region, provided by the Hadley Centre.

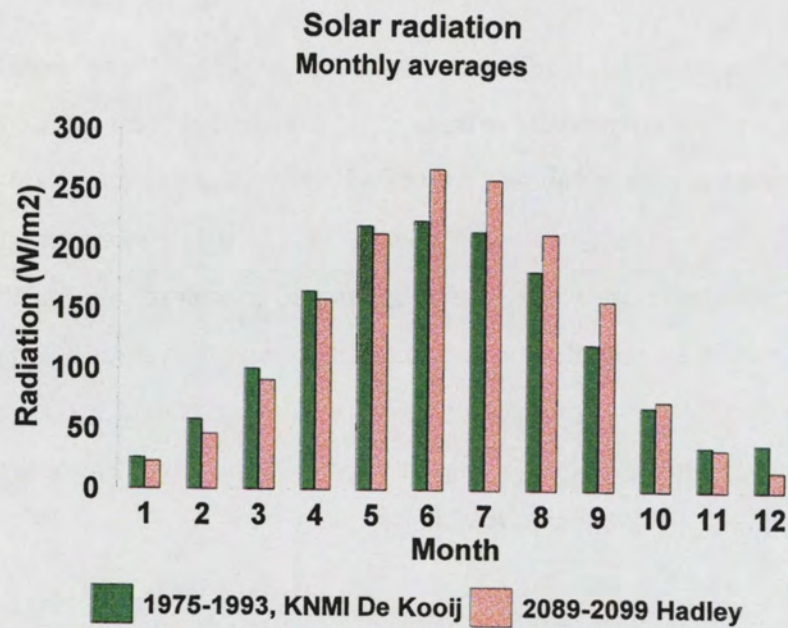


Fig.2.6 Monthly averages for solar radiation. Present values from Station De Kooij Airport (Den Helder), future values from Hadley Centre.

shown in Fig.2.6.

Some differences can be observed, but it is not clear whether this is an effect of the site, or of climate change. Summer values tend to increase, whilst winter values decrease somewhat. For our scenario analyses, these differences have been omitted.

2.4.7 Precipitation

As a consequence of climate change, it is expected that in our regions, precipitation will increase, especially during winter. A typical value reads 6% increase in the winter season; and this values has been taken as basis for a precipitation scenario. It is assumed that the fresh water inflow from Lake IJssel increases during the month October - March. It is also assumed that the nutrient content of the fresh water remains unchanged, although this may lead to a slight overestimation of eutrophication effects. Maximum values (Können et al, 1997) give 25% increase in 2100 during the winter period, while summers show a decrease.

2.4.8 Auxiliary effects

Not only effects that can be considered as more or less direct effects of changing weather conditions, like the ones mentioned above, but also some second order effects may be of importance. Backhaus (1993) mentioned a possible changing North Sea water circulation pattern, resulting from a relatively small change in average wind directions. The present overall circulation pattern is one that causes an southwards flow along the Scottish and English coast, and a northwards flow at the eastern side of the North Sea basin. A change of the average wind direction to more northern winds may influence this pattern thus that a more diverse pattern is created, or even a complete reverse pattern, where the northern water flow is at the western side of the basin. As a result, the boundary conditions for the Wadden Sea may become completely different from the present ones, and consequently, the system characteristics may differ significantly from what they are now.

2.4 Resume

In the above sections, the major steering factors for the Wadden Sea system, affected by climate change, are mentioned. In the following chapters, and the final integration part, the outcome of the several sub- studies are to be coupled with these scenarios.

We choose as major possible changes:

- a temperature increase: 4 °C overall, and some sub-scenarios with only milder winters and same temperatures during summer (chapter 3,6,7,8,9)
- an average water level increase of 20-60 cm (chapter 3,4,5,6,8,9)
- a change in water circulation patten, causing other water quality boundary conditions (chapter 9)
- increase in storm surge intensities. Frequency changes are not considered (chapter 4,9)
- increase in average wind speeds (chapter 4,9)
- changes in solar radiation have not been considered
- changes in precipitation (chapter 9)

Not all effects are taken into account for all the sub-studies, since not every combination is relevant. The number of the chapters are mentioned.

3 STEADY STATE IN A WADDEN SEA SYSTEM: A FIRST ESTIMATION OF CLIMATE CHANGE EFFECTS

3.1 Introduction

Climate change could effect a tidal system like the Dutch Wadden Sea in several ways. A temperature increase and a sea level rise are the two most striking phenomena. Additional effects could be a change in fresh water and/or nutrient inflow, occurrence of species that are known from warmer regions until now, and a change in predation pressure by migrating birds due to different migration patterns or changing predation possibilities.

Based on a steady-state approach for the western Wadden Sea system, a first estimate is given of the effects of changing temperature, nutrient and fresh water inflow. Also the effect of changing bird predation is on a long term steady-state situation in the Wadden Sea. Such a steady-state assumes that boundary conditions, nor the system characteristics change with time. Thus, all the rates (changes of algae content, benthic biomass, etc.) Are assumed to be zero. Or, in other words: all the basic differential equations are set to 0.

Such an approach is used more often in system analysis (..); the results give a first insight in how the dynamic system may response to certain changes in input variables or steering factors. The approach can also be applied in order to get some idea of the importance of model parameters. Finally, dependencies can be investigated: the steady-state method may serve as a tool to find final values for e.g. algae content and benthic biomass limits.

In order to perform such an analysis, the basic equations applied in the dynamic ecosystem model EcoWasp have been rewritten to a steady-state solution; at the same time, they are simplified a lot. In text box 3.1, an overview of the algae and benthic fauna equations is presented, as well as of the steady-state solution.

Average input data are available, as are average data for temperature, solar radiation, etc. Parameter values are partly derived from literature, and tuned by EcoWasp simulations and by

comparing results with field data and laboratory experimental data.

3.2 Basic equations

As an outline, basic equations for algae and filter feeder dynamics are given in text box 3.1a. The quasi steady-state solutions are obtained by setting all first derivatives equal to 0.

The result does not give information on a detailed scale (time, space, population), but serves quite well to get rough information on what could be expected on a whole system scale. In text box 3.1b, the steady state solution for such a simplified set of equations is given.

Although not shown, the set of equations also covers a detritus and nutrient steady state, and includes terms for predation upon shell fish by birds, extraction of shell fish by fisheries and extra predation by crabs and star fish.

Input of matter from the North Sea and the fresh water Lake IJssel is implemented.

The light limitation function for algae growth is according to Smith, (see e.g. Brinkman 1993), with I_k as Smith-constant; suspended particles (algae, detritus) contribute to the extinction coefficient of the water column. An average [inorganic solid] is used to cover the effect of silt and sand.

One of the first conclusions one can draw from such a steady-state is that for example the steady-state algae content in the Wadden Sea does not depend on the concentration of algae at the North Sea boundary: Any increase is consumed completely by filter feeders, and vice versa, and thus, it affects filter feeder biomass only. One can also read that algae concentrations in the Wadden Sea certainly does depend on filter feeder characteristics. When the main filter feeders in the Wadden Sea are replaced (for whatever reasons) by other species, with different filtration characteristics, consequently the [algae] will change.

And thus, the primary production does depend on the rate constant for algal growth, and the rate constants for filter feeder removal or mortality.

Roughly, algal dynamics read

$$\frac{dA}{dt} = k_p A - k_d A - k_g A G + \frac{Q}{V} (A_{ext} - A) \quad (\text{g alg m}^{-3} \text{ day}^{-1}) \quad (3.1)$$

with

- A = algal content (g DW m⁻³)
- A_{ext} = algal content in input water (g DW m⁻³)
- G = grazer content (g DW m⁻³)
- Q = input or exchange volume (m³ day⁻¹)
- V = volume (m³)
- k_p = algal production parameter (day⁻¹)
- k_d = algal respiration parameter (day⁻¹)
- k_g = grazing parameter (m³ gram⁻¹ mussel day⁻¹)

For mussel growth:

$$\frac{dG}{dt} = \gamma k_g A G - k_r G - k_m G \quad (\text{g mussel m}^{-3} \text{ day}^{-1}) \quad (3.2)$$

- k_r = mussel respiration parameter (day⁻¹)
- k_m = mussel mortality parameter (day⁻¹)
- γ = food efficiency (g mussel g⁻¹ algae)

Mussels are computed as biomass per unit volume.

Text box 3.1a Basic equations for algae and filter feeder dynamics

Thus, with

$$y_1 = k_p - k_d - \frac{Q}{V} \quad (3.3)$$

and

$$c = + \frac{\omega}{V} A_{ext} \quad (3.4)$$

and

$$y_2 = -k_r - k_m \quad (3.5)$$

it follows that

$$0 = y_1 A - k_g A G + c \quad (3.6)$$

and

$$0 = \gamma k_g A G + y_2 G \quad (3.7)$$

have to be solved. (3.7) directly gives, since G can be removed right away,

$$A = - \frac{y_2}{\gamma k_g} \quad (3.8)$$

Substitution into (3.6) gives

$$G = \frac{y_1}{k_g} + \frac{\gamma c}{y_2} \quad (3.9)$$

Text box 3.1b Steady state solution of the predator-prey equations (2) and (3)

3.3 Considered area

The computations and morphological data all consider the western part of the Dutch Wadden Sea. It was not useful to take the whole Wadden Sea area into account, since it cannot be considered being well mixed and uniform. Therefore, from a modelling point of view, it would be necessary to perform different computations for each of the tidal basins. For the western part we have relatively many data at our disposition, although the number still is quite limited regarding the many variables and processes taken into account.



Fig. 3.1 Wadden Sea in the Netherlands

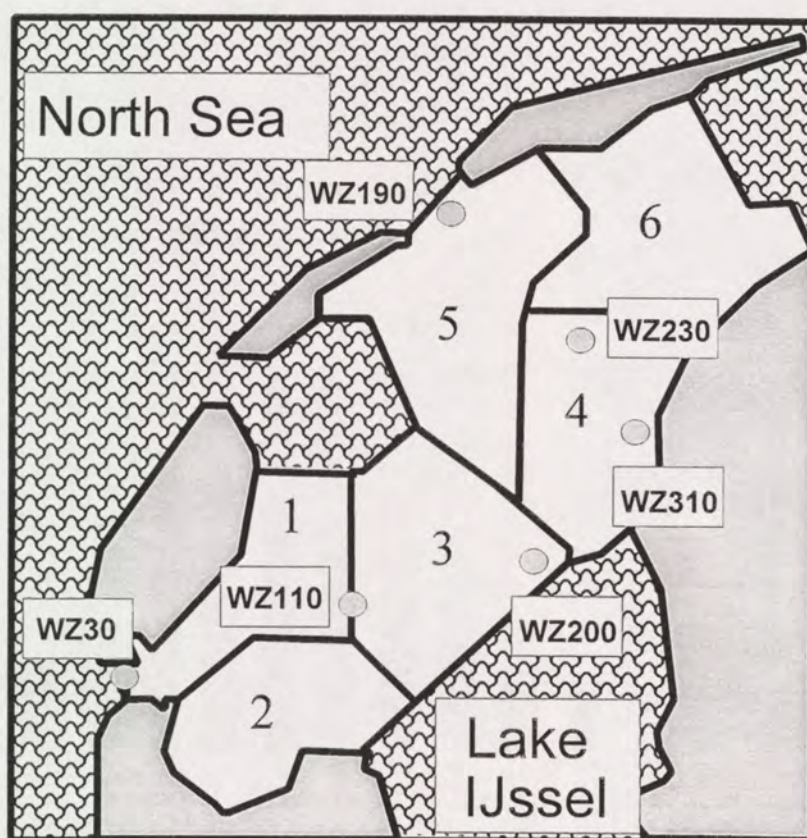


Fig. 3.2 Western part of the Dutch Wadden considered in the computations. Data points show RIKZ monitoring stations. Compartments are not considered in the present exercises, but are used for EcoWasp computations.

Callantsoog 002

Algae-dry weight

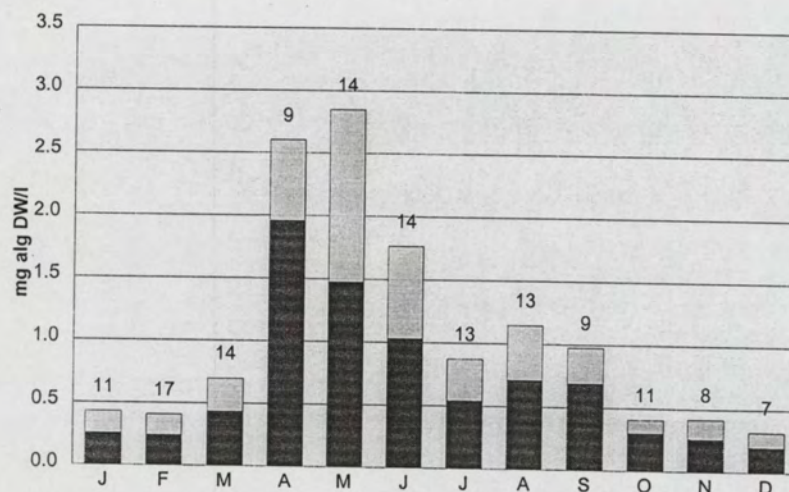


Fig. 3.3 Monthly averages for North Sea algae dry weight. Location Callantsoog, 2 km from coast. Data from Rijkswaterstaat (1976-1996). Dark = average, grey = standard deviation

Waddenzee 230

Algae-dry weight

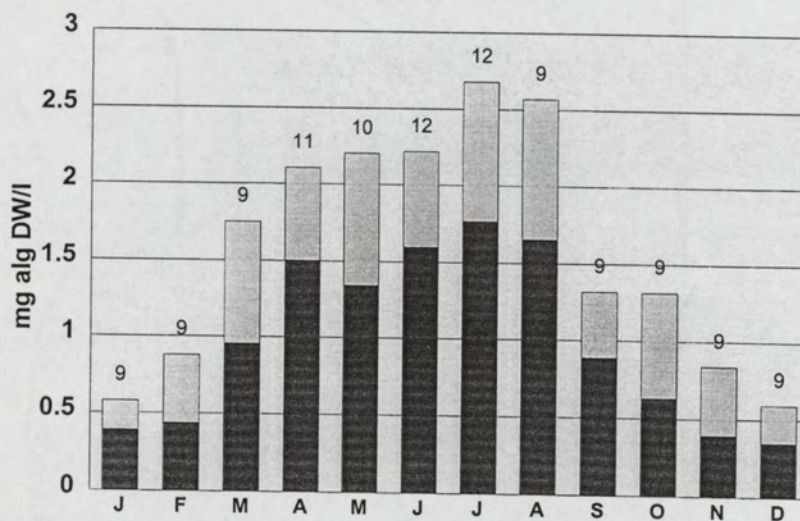


Fig. 3.4 Monthly averages for Wadden Sea algae dry weight. Location WZ230 (see Fig. 3.2). Data from Rijkswaterstaat (1976-1996). Dark = average, grey = standard deviation

3.4 Available data for input and for comparison

3.4.1 Algal concentration in the North Sea, at other boundaries, and in the Wadden Sea

Data for the input from the North Sea, from Lake IJssel, and for the Wadden Sea are available from the Rijkswaterstaat monitoring activities; every month water quality sample are taken at several locations. Algae data, derived from chlorophyll-a analysis, show an average North Sea value of 0.67 ± 0.53 (Fig. 3.3, Location Callantsoog 002). Location Callantsoog 001 (1 km from the coast) gives similar values, location 004 shows lower values (0.43 ± 0.34). This value decreases with increasing distance to the shore.

Algal concentrations are available from the Rijkswaterstaat monitoring activities; every month water quality sample are taken at several locations. Algae data, derived from chlorophyll-a analysis, show an average value between 0.8 and 1.3 g m^{-3} (0.99 ± 0.53) for an inside location (Fig. 3.4) and between 0.7 and 1.0 g m^{-3} (0.82 ± 0.38) for a site more close to the North Sea (site WZ 110). As an average value, 0.90 g m^{-3} seems appropriate.

For both estimates of algae contents, an approximation of the chlorophyll-content of algae of 1.2% (relative to dry-weight) has been used.

There is no input from algae by the fresh water; all fresh water algae are assumed to be detritus.

3.4.2 Detritus concentration

See 3.4.1 for the source. Average data cannot be obtained directly from the monitoring results, but have to be estimated from total organic matter, estimates for algal concentrations, total particulate matter and glowing rests, and data for P- and N-contents (also dissolved, total, total organic) and estimates for P- and N-content of algae and detritus. It is not relevant to explain this procedure, but following such methods, it is possible to derive dissolved and particulate detritus contents of the Wadden Sea and the North Sea. As an extra result, it turned out that most of the detritus (particulate and dissolved) probably is humic-like matter; during the summer period there is an increase in organic dissolved matter, which can be contributed to more reactive components.

For WZ230 the average detritus content is 8.5 ± 2.2 and $9.7 \pm 4.1 \text{ g m}^{-3}$, for WZ110 it is 6.6 ± 2.7 and $6.4 \pm 2.8 \text{ g m}^{-3}$.

3.4.3 Nutrients

For the computations in this chapter, only phosphorus and nitrate + ammonium (as basic N-sources) have been considered. Average values for Callantsoog 002 are: ortho-P: 1.4 mmol m^{-3} (± 0.7), total P: 4.1 mmol m^{-3} (± 1). NO_3^- : 28 mmol m^{-3} (± 15), NH_4^+ : 5.8 mmol m^{-3} (± 1.8).

Average Wadden Sea values : ortho-P: 1.7 mmol m^{-3} (± 0.4), total P: 5.3 mmol m^{-3} (± 0.7). NO_3^- : 33 mmol m^{-3} (± 34), NH_4^+ : 9.3 mmol m^{-3} (± 4.3).

3.4.4 Benthic fauna

Benthic fauna densities are known for recent years from yearly inventories by the RIVO-fishery research institute (eg. Van Stralen, 2000), and before that from extrapolations based upon local investigations. V/d Veer (1989) gives $8.3 \text{ g AFDW m}^{-2}$ of mussels alone, and mentions that this is about 38% of total biomass present. For culture plots, he mentions biomass densities of about $250 \text{ g AFDW m}^{-2}$ average. Wild mussel beds show densities of about $800 \text{ g AFDW m}^{-2}$ when lots of macroalgae are present, and up to $1400 \text{ g AFDW m}^{-2}$ when there is little or no vegetation present (Gätje & Reise, 1997).

At the western Wadden Sea culture plots (70 km^2 in the years from 1960, $250 \text{ g AFDW m}^{-2}$), about $17.5 \cdot 10^6 \text{ kg AFDW}$ mussels is present.

RIVO-inventories in the years 1992-2000 (e.g. Van Stralen, 1998; Van Stralen & Kesteloo-Hendriks, 1998) show an average cockle biomass of $8 \cdot 10^6 \text{ kg AFDW}$ in the whole Wadden Sea, which equals $3.2 \text{ g AFDW m}^{-2}$. In 1998 and 1999, this figure is about 2 to 3 times as high as a result of the very good recruitment in 1997. Densities are up to $7\text{-}10 \text{ g AFDW m}^{-2}$, but mussel densities were considerably lower.

Combining most data, average biomass densities of $10\text{-}20 \text{ g AFDW m}^{-2}$ seem to be normal for benthic filter feeders (the latter being the optimistic one); and these values are used as comparison for the computations.

3.4.5 Primary production

There are few data on primary production available. In 1979 and 1986, the NIOZ performed an intensive research in the western Wadden Sea. Primary production data (EON-I, 1988; EON-II, 1988) are given in $\text{g m}^{-2} \text{y}^{-1}$, but it is not completely clear how such an extrapolation has been performed from the real measurements. Also, most data come from incubation experiments, where interpretation to field production data is done by the application of an empirical formula:

$$P = 0.5 P.E.D \quad (3.10)$$

with P = mean incubator primary production ($\text{g m}^{-3} \text{h}^{-1}$), E = depth of euphotic zone (m), D = daily light period (h d^{-1}). This method contains a lot of possible extrapolation inaccuracies. Values range from 100-340 $\text{g C m}^{-2} \text{y}^{-1}$, ie. 250 - 850 $\text{g DW m}^{-2} \text{y}^{-1}$ as pelagic primary production; the estimates for the 70's read 145 - 200 $\text{g C m}^{-2} \text{a}^{-1}$, or 360 - 500 $\text{g DW m}^{-2} \text{a}^{-1}$. The lower values are mentioned for the inner part of the Wadden Sea area, the higher ones (about 20-40% higher) for the Marsdiep area (the tidal inlet between the island of Texel and the main land). The data for the 80's are 750 - 1100 $\text{g DW m}^{-2} \text{a}^{-1}$; the EMOWAD simulations (EON-II, 1988) show primary productions of 550-1000 $\text{g DW m}^{-2} \text{a}^{-1}$, the lower values for the inner compartments. In Table 3.1, some values are summarized.

Table 3.1 Western Wadden Sea pelagic primary production data from literature

Year	Production ($\text{g DW m}^{-2} \text{y}^{-1}$)		Reference
	Inner side	Outer side	
1963 - 1966	300	425	Postma & Rommets (1970)
	230	375	Cadée & Hegeman (1974b)
1972 - 1937	375 - 500		Cadée & Hegeman (1974b)
			Cadée & Hegeman (1979)
1974 - 1975		340 - 360	Cadée & Hegeman (1979)
1981 - 1982		850	Cadée (1986)
1985		650	Cadée (1986)
1986	410	750	Veldhuis et al (1988)

Philippart & Cadée (2000) made an overview, and included estimated production by using regression based formulas, that relate system primary production to nitrogen input. She gave values of $750 \text{ g DW m}^{-2} \text{ y}^{-1}$ in the mid-1970's, $850 \text{ g DW m}^{-2} \text{ y}^{-1}$ in the mid-1980's, and around $800 \text{ g DW m}^{-2} \text{ y}^{-1}$ during the early 1990's. Benthic primary production was estimated at 250, 175 and $225 \text{ g DW m}^{-2} \text{ y}^{-1}$ respectively (these data are less reliable because they are computed as the difference between total and pelagic primary production). According to these figures, these values are too high for the 70's, where, according to Philippart & Cadée, primary production was limited by P and not by N. Macroalgae did not contribute significantly to the primary production in this period.

3.5 Process characteristics

3.5.1 Predation pressure by birds

Mortality caused by birds might be an important factor for the structuring of macro fauna assemblages, or even the limitation of macro benthic biomass. Oystercatchers and Eider Ducks are regarded as the most important benthic shell fish predators in the system (Swennen, 1976; Zwarts, 1996; Ens, 2000). Their body weight is estimated as 550 and 2000 g, respectively (or 110 resp. 400 g DW). Their daily prey consumption is estimated at $0.4 \text{ (g g}^{-1} \text{ day}^{-1})$. For Oystercatchers, this has been studied intensively, resulting in $2 \cdot 10^{-3} \text{ prey s}^{-1} \text{ ind}^{-1}$, with $0.5 \text{ g DW prey ind}^{-1}$. This gives $40\text{-}45 \text{ g DW Oystercatcher}^{-1} \text{ day}^{-1}$, or $200 \text{ g flesh weight day}^{-1}$, and $800 \text{ g fresh weight day}^{-1}$ (see e.g. Ens, 2000). For Eider Ducks, a daily average consumption of 600-800 gram flesh per $\text{ind}^{-1} \text{ day}^{-1}$ is assumed, according to Swennen (1976) and Nehls (1995). This also is $0.3\text{-}0.4 \text{ g g}^{-1} \text{ day}^{-1}$.

As a yearly average, 100.000 Oystercatchers and 60.000 Eider Ducks are present in the Dutch Wadden Sea. Maximum numbers are higher: Eider Duck summer numbers are about 30.000 for the nineties, and winter numbers are 100.000 - 160.000 (Camphuysen 1996). Oystercatchers are present with lower numbers of about 20.000-30.000, and maximum numbers of about 250.000 birds. Average value ranges from 100.000-150.000 (Meltote et al, 1994; Smit & Zegers, 1994).

3.5.2 Predation pressure by starfish and crabs

One aspect that is fairly unknown concerns the effect of starfish (*Asterias rubens*) and crabs (mainly *Carcinus maenas*). Both are capable of eating shellfish, the size depending on the size of the predator. *C. maenas* is rather small, and will restrict itself to really small shells. There is little known about the number of starfish and crabs in the system, nor about their sizes. For an about 10 cm arm length starfish, Saier (2001) found a food demand of about 1 medium sized mussel per 3-5 days; which is about 0.1-0.2 g AFDW per animal per day. She found that only in exceptional cases (high seastar abundances), seastars are capable of structuring sub-tidal mussel beds. Seed (1992) mentioned a structuring effect of starfish feeding on smaller sized mussels in a mussel culture plot. The effect probably was not purely negative; possibly such a predation might create better feeding conditions for the larger, untouched, mussels.

Crabs are capable of consuming the smaller size classes of cockles (<20 mm, Seed, 1992); after Sanchez-Salazar et al (1987), he mentioned that crabs may consume up to 80 cockles m⁻² month⁻¹, in sub-tidal areas.

What lacks in our Wadden Sea situation is that very few data are available on densities of starfish and crabs. They may be numerous, but usually this is a local situation. A whole system overview is not available at this moment. Only after better data on numbers and sizes become available, one could come to better food demand estimates. Until then, only scenarios of an overall food demand can be used here; the coupling to reality remains unclear.

3.5.3 Other mortality

A major mortality cause for filter feeders in the Wadden Sea is related to physical phenomena, like storms and water currents and ice. The effect of both first factors has never been quantified very well; on the mass budget of filter feeders, it is a highly unknown term. Overall winter survival, including all possible factors, has been estimated by Beukema (1985). For cockles, he mentioned a relative winter survival may range from almost 0 to about 70 %. Especially cold winters may cause high mortalities; cockles are relatively susceptible to freezing conditions.

Mussels and Baltic Tellins suffer much less from cold, but mussel beds may be severely damaged by floating ice.

3.5.4 Assimilation efficiency of filter feeders

During preliminary computations with this steady-state description, it turned out that the assimilation efficiency of filter feeders (how efficient can algae be transformed into filter feeder tissue) is a key factor in such a steady state model. The BOEDE-model (Baretta & Ruardij, 1988) uses 0.8 as average value. Begon, Harper & Townsend (1990, following Heal & MacLean, 1975) give for vertebrate herbivores 0.5, for invertebrates 0.4. Invertebrate decomposers reach 0.2. Carnivores come up to 0.8, but for the filter feeder system in the Wadden Sea this is not a relevant value. Kersting (pers com) mentioned also a factor of 0.8 for daphnids; Smaal & Twisk (1997) measured (following Conover's AFDW-method) $0.37 (\pm 0.13)$ - $0.47 (\pm 0.06)$ for mussels *Mytilus edulis*, depending upon food (*Phaeocystis* and *Phaedactylus*, respectively, as food source). Conover (1966) measured for *Calanus hyperboreus* a value of 0.13-0.17. Thus, an average value of about 0.4 seems to make sense as starting point for the computations with varying single parameter values.

3.5.5 Filtration and respiration rates of filter feeders

Basically, filter feeder filtration and respiration parameters cannot be estimated separately from any steady state-like description, simply because one only deals with the resultant of both processes. However, separate EcoWasp dynamical computations (chapter 9), where growth of individuals is computed, combined with literature data on mussel activities reveal values that also result in a realistic yearly individual growth rate. Also, computed uptake rates of chlorophyll-a fit very well to field measurements, as well do computed and measured exchange rates of ammonium and phosphorus (Asmus & Asmus, 1997). In chapter 9, the process of filtration, respiration and growth has been explained in more detail; here we restrict ourselves to a short overview of applied parameter values (Table 3.2).

3.6 Parameter values

Based on the descriptions given above, basic parameter values are summarized in Table 3.2. Data on the exchange rates between North Sea and Wadden Sea are from Ridderinkhof (1988). Morphological data have been derived from Rijkswaterstaat depth measurements (RIKZ, 1998).

Table 3.2 Basic values for parameters and western Wadden Sea system characteristics

Parameter	Name	Value	Unit
Average depth	Hav	2.83	m
Volume	Vol	3.69E+09	m ³
Inflow from North Sea	Qsea	6.18E+08	m ³ /day
Inflow from Lake IJssel	Qfresh	4.20E+07	m ³ /day
Outflow to North Sea	Qout	6.60E+08	m ³ /day
Uptake rate constant algae	kpa	2.00E+00	1/day
Respiration rate constant algae	kda	2.00E-02	1/day
Mortality rate constant algae	kma	2.00E-03	1/day
Temp-function algae growth	f(F,1)	1	(-)
Temp-function algae respir	f(T,2)	1	(-)
Temp-function algae mortal	f(T,6)	1	(-)
Filtration rate constant filter feeders	kgg	4.00E-02	m ³ /gram/day
Respiration rate constant filter feeders	krg	1.20E-02	1/day
Mortality rate constant filter feeders	kmg	1.20E-02	1/day
Temp function filter feeder filtration	f(T,3)	1	(-)
Temp-function filter feeder respiration	f(T,4)	1	(-)
Temp-function filter feeder mortality	f(T,5)	1	(-)
Filter feeders eaten per bird	kbb	4.00E-01	g/g/day
Filter feeders per Starfish+Crabs	ksf	4.00E-01	g/g/day
mineralization rate constant detritus	kmin	6.00E-04	1/day
Temp-function detritus decay rate	f(T,7)	1	(-)
fraction of algae ending as detritus	beta AD	1.00E-02	(-)
fraction of filter feeder ending as detritus	beta GD	1.00E-03	(-)
Average residence time of the system	tau	5.59	day

Table 3.2 (continued) Basic values for parameters and western Wadden Sea system characteristics

Temp-function filter feeder mortality	f(T,5)	1	(-)
Filter feeders eaten per bird	kbb	4.00E-01	g/g/day
Filter feeders per Starfish+Crabs	ksf	4.00E-01	g/g/day
mineralization rate constant detritus	kmin	6.00E-04	1/day
Temp-function detritus decay rate	f(T,7)	1	(-)
fraction of algae ending as detritus	beta AD	1.00E-02	(-)
fraction of filter feeder ending as detritus	beta GD	1.00E-03	(-)
Average residence time of the system	tau	5.59	day
Phosphorus content of algae	gamA	2.3E-04	mol/g
Phosphorus content of filter feeder	gamG	2.3E-04	mol/g
Phosphorus content detritus	gam_D	8.7E-05	mol/g
Area Western Wadden Sea	West WS	1.3E+09	m2
[Detritus] North Sea water	DetNS	8.0E+00	g/m3
[ALG] North Sea water	AlgNS	6.7E-01	gram/m3
[Nutrient] North Sea	N_NS	1.5E-03	mol/m3
[Nutrient] Lake IJssel	N_IJ	3.0E-03	mol/m3
[Detritus] Lake IJssel	DET_IJ	1.3E+01	g/m3
basic extinction coefficient water	ext0	2.0E-01	m-1
Average [Inorganic Solids] WWS	Sol	5.2E+01	g/m3
Fishery ton/year	Fish	1.4E+08	g DW/y
Total biomass birds	Birds	3.5E+07	g DW / WS-system
Starfish + Crabs	StarFish	0.0E+00	g/m3
Monod-constant for algae growth	MONOD	9.00E-05	mol/m3
Oystercatchers		1.00E+05	Number/system
Eider ducks		6.00E+04	Number/system
Fraction dry weight in shell		5.00E-02	g/g
Fraction Light period per day		1.00	Day/day
Smith constant algae	SMITH	1.0E+01	W/m2
Average solar radiation	I_av	1.2E+02	W/m2
Eider duck-weight	AFDW	400	gr AFDW/ind
Oystercatcher-weight	AFDW	110	gr AFDW/ind

Bird weights are from Glotz et al, AFDW is taken as 20% of total individual mass weight

3.7 Numerical investigations

3.7.1 Computed situations

With the parameter values mentioned above as starting point, a number of computations has been performed. The aim was to examine the effects of

- temperature effects
- the algal concentration at the North Sea boundary
- predation pressure by birds, fisheries and what we called ‘Starfish+Crabs’, ie all the epibenthic predation upon shellfish, and other mortality reasons
- inflow of fresh water
- average system depth
- algal growth parameter choices
- food efficiency of filter feeders (assimilation efficiency, or the part of ingested food that is taken up by the body, and is not excreted as faeces)
- filter feeder parameter choices (filtration capacity, respiration parameters)

The three latter computations serve two goals. First, they are needed to test the parameter choices and find the most appropriate combination. Second, they will give an idea of what can be expected if other species with other growth and feeding characteristics than the present algae and filter feeders become dominant. Especially the effects of a Japanese Oyster invasion can be sketched. The species has a much larger specific filtration rate than the Blue Mussel or Cockle, and it is capable to out compete mussels partly or even completely. E.g., in the Dutch Delta (Easter Scheldt estuary) the species has become the dominant intertidal filter feeder.

3.7.2 Results

Varying the temperature function value

An increase in temperature function (Fig. 3.5a,b) value results in an increase of the filter feeder biomass, of detritus contents and of primary productivity. The algae content is not very sensitive

to changes in temperature, because any change in algae production rates is used completely by filter feeders. Therefore, the end-organisms show most of the effects.

Although the steady state situation is not very affected by T-variations, many characteristics deal with seasonal variations. This analysis is restricted to biomass and production; recruitment and other processes do show a close relationship with temperature variations (chapter 7) and will cause system changes whenever they become reality.

Fig. 3.5a,b also shows that the computed filter feeder biomass density is above the observed range. The reason probably is that in the real world, the maximum value, which is how this steady state value has to be read, will hardly be reached. Or, in other words, on average there will be a large(r) loss factor. This loss may have to do with negatively influenced by a lot of factors, like winter conditions, predation upon larvae by shrimps, and storms flushing away freshly build mussel beds.

Varying the average system depth

In advance, one would expect that an increase in depth would generally induce an decrease in primary production, and an increase in food availability for filter feeders. But, from the computations it became clear that varying system depth has only very limited over-all meaning for the system's behaviour (Fig. 3.6). Primary production hardly changes, nor does the algae content of the Wadden Sea, and consequently, according to the present computations, there is little effect upon filter feeder total biomass.

Nitrogen as main nutrient instead of phosphorus

The same computations have also been performed with nitrogen ($\text{NO}_3^- + \text{NH}_4^+$) as nutrients, instead of phosphorus, but this gave only small differences. This indicates that on average, neither P or N can be regarded as *the* main limiting nutrient. In these steady state exercises, there is hardly any effect of nutrient limitation. In reality, where seasonal variations play an important role, nutrient limitations start to be important because maximum growth potential coincides with a minimum of nutrient supply (Chapter 9).

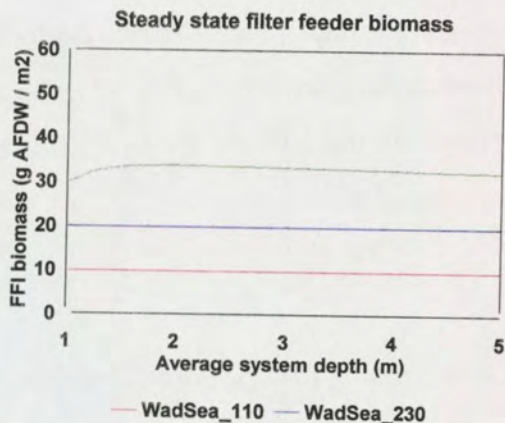
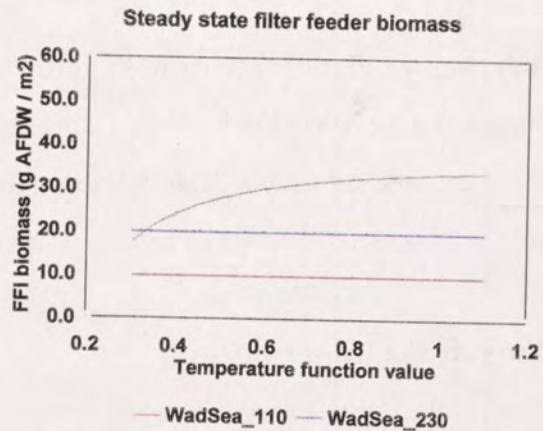
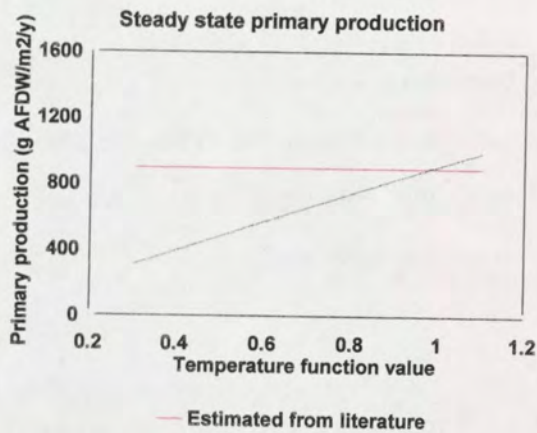


Fig. 3.5a Temperature effects on primary production
Fig. 3.5b Temperature effects on filter feeder biomass

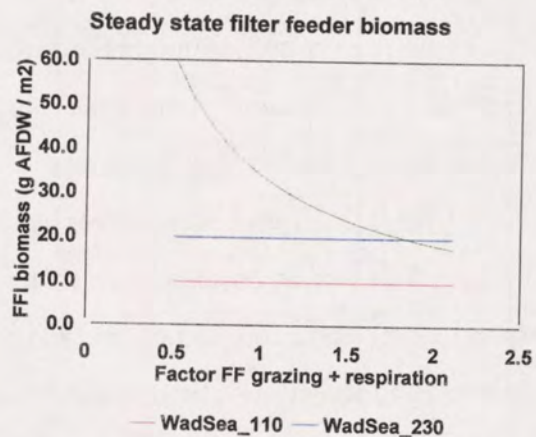
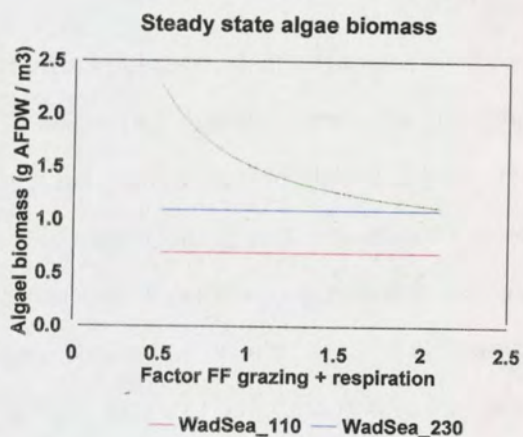
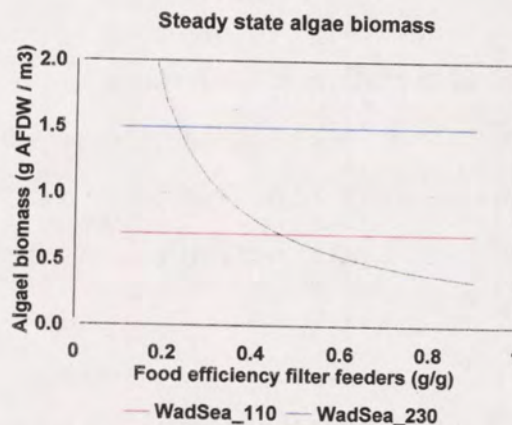
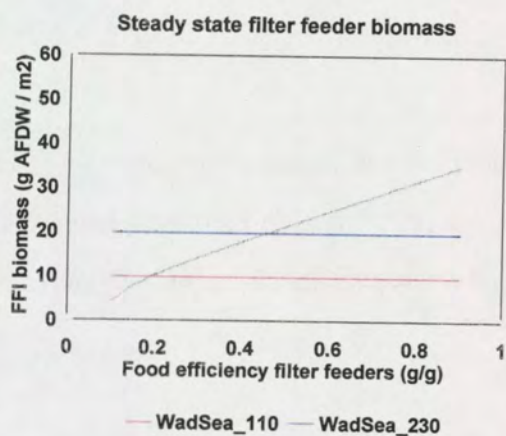
Fig. 3.6 Effect of system depth on filter feeder biomass

Fig. 3.7a Effect of food assimilation efficiency of filter feeders on steady state biomass density

Fig. 3.7b Effect of food assimilation efficiency of filter feeders on primary production

Fig. 3.8a Effect of filter feeder filtration and respiration rate on primary production

Fig. 3.8b Effect of filter feeder filtration and respiration rate on steady state biomass density



Varying the algal concentration at the North Sea boundary

Increasing the North Sea boundary algae concentration affects filter feeder biomass directly. Also nutrient concentrations and detritus contents increase, but not algae content and primary production. Any increase in algae availability is consumed by filter feeders.

Varying the fishery intensity

The result is not very sensitive to slight changes in fishery intensities. Only when the extraction (or read: mortality by whatever causes) is an order of a magnitude higher than 5000 ton flesh year⁻¹, some system characteristics respond. Filter feeder biomass decrease (of course), while steady state nutrient concentrations come close to the average observed values. Primary production and algae biomass increase only slightly, as does the detritus biomass.

Varying the predation pressure by birds

Increasing bird predation pressure is a process similar to increasing fishery extraction, although there are slight differences.

Varying the inflow of fresh water

An increase in fresh water input decreases the filter feeder biomass, because it negatively affects algae availability. Algae contents are not affected; nutrient concentration increases, because of an increased input. Since detritus input increases too, its content in the Wadden Sea increases slightly.

Varying the nutrient concentration in the fresh water inflow

Increasing nutrient concentration in the fresh water input flow only affects the average nutrient concentration itself. Reason is that in the steady state computations, there is hardly any effect of nutrient limitation visible: nutrient limitation of plankton growth is only present in a dynamical situation. This is confirmed more or less by the yearly observations: it is also Si that reaches low values first, followed by an abundance change from diatoms towards non-diatoms. Nitrogen and phosphorus both reach low values, and sometimes it seems that N is the relative lower one, and sometimes P. Since fresh water contains much larger amounts of N (compared to P) than North

Sea water does, it is plausible that the inflow quantity of fresh water during the growing season will largely determine whether N or P will limit algae growth.

Varying the assimilation efficiency of filter feeders

The result of the steady-state computations is sensitive to the filter feeder assimilation efficiency (Fig. 3.7a,b). The 'standard' value from table 3.2 results in a slightly too high mean algae concentration, and a nutrient content (based upon phosphorus as main nutrient) that is too low. It is mainly the steady state filter feeder biomass that is high compared to the observed values. This turned out to be the tendency for all computations. Computed primary production is about $700 \text{ g DW m}^{-2} \text{ y}^{-1}$, which fits the observations satisfactorily.

Varying the filter feeder parameter choices

The steady state result is very sensitive to changing parameters describing filter feeder activities (Fig. 3.8a,b). One effect (assimilation efficiency) has already been mentioned above. An increasing filtration and respiration rate results in lower algae contents; the turnover rate increases, and this acts as a loss factor for algae. Also, both filter feeder biomass and primary production decrease. It is this exercise that is exemplary for the introduction of other species, like the Japanese Oyster, which species does show a higher filtration rate than the Blue Mussel does.

Varying the algal growth parameters

An increasing algae growth rate constant does not influence the [algae] in the Wadden Sea, but only affects [filter feeders], primary production, and to a lesser extend, [detritus].

3.8 Discussion

From the examples given in section 3.6, it is obvious that there are a couple of factors that significantly contribute to whole system characteristics. It is concluded that assimilation efficiency probably should be around 0.4, otherwise most of the results would be out of scope. Also, the filtration and respiration parameter settings turned out to be important, although precise

values cannot be estimated accurately enough from steady state model computations. The net individual growth is never part of such computations, and it is this response that is used in dynamic computations that is used to test the adequateness of the chosen parameter values.

Fresh water input nor varying fresh water or North Sea nutrient concentrations induce important changes in the steady-state Wadden Sea ecosystem. North Sea algae content exclusively serves as extra food source for benthic filter feeders, and does not affect algae concentration in the Wadden Sea.

Temperature increase only slightly affects benthic filter feeder densities, as a consequence of increasing primary productivity.

Computed filter feeder densities are a lot higher than observed densities. Reason for this is probably that these results indicate maximum values, while in nature many other factors also contribute to a much higher mortality. Increasing mortality (man-induced, like fisheries, or otherwise, like shrimp predation on larvae, storm losses of mussel beds) gives more realistic densities as well as more realistic nutrient concentrations. Possibly, a far from ideal is something that may really limit filter feeders abundance.

Although solids have not been included in the present computation exercises, solid catchment can be estimated, which will equal maximum solid deposition. This maximum is estimated following $dSol/dt=0 = \text{-filtration} + \text{input} - \text{output}$. Without internal regeneration of suspended solids *and* without explained the computation completely, it follows that the maximum filtration rate is about $2\text{-}3 \text{ g m}^{-3} \text{ d}^{-1}$, or $5\text{-}9 \text{ g m}^{-2} \text{ d}^{-1}$, or, with an average sediment density of 2.5 kg m^{-3} , the maximum biogenic sedimentation is $2\text{-}3 \text{ mm d}^{-1}$. In areas with mussel beds, this figure will be much higher; resuspension will reduce the net sedimentation considerably.

4 EFFECTS OF SEA-LEVEL RISE ON SALT MARSHES AND TIDAL FLATS

4.1 Introduction

During the NRP-I project, Houwing et al. (1995) studied the boundary conditions for the development of salt marshes, integrating the hydrodynamics, the morphodynamics and the biologic constraints. In addition, relationships were established between salt marsh extension, sea-level rise and the connected hydro-meteorological conditions. This resulted in a qualitative model for salt marsh development as the result of sea-level rise. This model is verified by some empirical relationships. Using this model it appeared that under sound management conditions the salt marshes along the mainland coast of the Wadden Sea appear to be able to keep pace with rising sea-level through vertical accretion, if the sediment supply is sufficient. However, the reliability of the model is seriously restricted. It is based on empirical data, gained by measurements at a very small site within the sedimentation fields of the Groninger coast. In addition, as a result of sea-level rise, the hydrodynamic conditions, especially the intensity of the tidal currents and the wave action may result in erosion. Furthermore, the estimate of the future sediment supply is uncertain and a lack of sediment could result in erosion and lowering of the salt marsh pioneer zone. Finally, mitigating measures to reduce the negative effects have not been studied in sufficient detail.

During this NRP-II project it has been investigated how the results of the study on the restricted test site of NRP-I can be extended to other salt marsh areas within the sedimentation fields (Fig. 4.1). The study focussed on the pioneer zone of the salt marshes, because this zone attains a very delicate balance between applied shear stress and the bed shear strength. Effects of changes in sea-level rise will firstly be noticed in the pioneer zone of the salt marsh. In addition, during the NRP-II project the test area included the shallow intertidal flats outside the sedimentation fields. When a positive accretion balance is maintained in the areas of the intertidal mudflat and the pioneer zone of the salt marsh there is no problem concerning sea-level rise (Dijkema et al., 1990; Houwing et al., 1995).

In the pioneer zone and on the tidal flats field experiments were conducted to provide data of the hydrodynamics and morphodynamics on sedimentation and erosion. The effects of mitigating measures such as techniques for wave and current reduction were encountered in

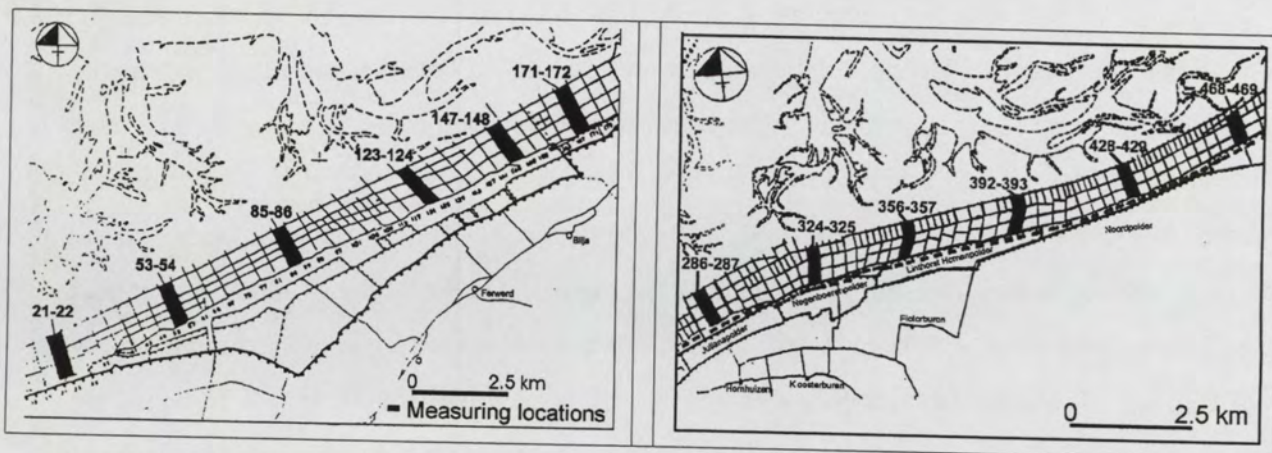


Figure 4.1: Measuring locations along the Dutch salt marsh coast; Friesland (left) and Groningen



Figure 4.2: Leveling instrument.

the study. Besides process knowledge and spatial variations, the role of storm events on salt marsh development was studied to determine the effect of an increase in storm frequency and duration during climatic changes. Another extension of the knowledge on salt marsh development was achieved by studying the effects of long-term changes in wind strength and water levels on salt marsh development. This part of the study was based on long term data of the Ministry of Water Management (Rijkswaterstaat) on height development, wind strength and water levels from 1965 until present.

4.2 Materials and methods

The four-year study period started with a literature study and the writing of a research proposal. For a period of two years field measurements have been executed. The measurements were followed by an extensive analyses period. Furthermore, a model study was done in a GIS (Geographical Information System) using long term Rijkswaterstaat data.

The field measurements in the pioneer zone included measurements of sedimentation and erosion using a leveling instrument (Fig. 4.2). The large scale morphology seaward of the pioneer zone was examined using hydrographic maps of the Wadden Sea. Characteristics of the sedimentation fields were obtained through grain size analyses of bed sediment samples, collected by a core slicer. Current and wave induced shear stress and suspended sediment transport were calculated using continuously collected data of the measuring frames. The instruments that were attached to the frames included pressure sensors, to measure water level fluctuations, electromagnetic flow meters (EMF) and sensors to measure suspended sediment concentrations (SSC-meter) (Fig. 4.3).

The long-term data analyses comprised salt marsh elevation data of the entire salt marsh area along the mainland coast, wind data and water level data. The elevation data, collected since 1965, were processed in a raster based Geographical Information System (GIS) called PCRaster (Van der Meer and Janssen-Stelder, submitted). The yearly collected elevation data were interpolated along the 50 km wide salt marsh coast. The geostatistical method 'universal kriging' was used for this interpolation. The interpolated maps of height, surface, volumes



Fig. 4.3: Measuring frame with pressure sensor, electromagnetic flow meter (EMF) and SSC-meter.



Fig. 4.4: Wave reduction by a brushwood groyne.

and seaward extension were created in the GIS model. Wind and water level data was available from a station in Lauwersoog from 1968-1998. From these wind and water level data the average, maximum and top 10% of the values were calculated. The top 10% values were used as a measure for storm frequency and strength. The water levels during the storm events (determined by the wind data) were also calculated.

4.3 Results

4.3.1 Spatial variability in erosion and sedimentation along the coasts of Friesland and Groningen

The interaction between sediment supply and hydrodynamic conditions, especially waves, determines the balance between sedimentation and erosion in the pioneer zone of the salt marshes. Along shore differences in hydrodynamics and sediment supply explain a significant part of the along shore variation in the height development of the studied sedimentation fields. Sediment supply appeared to be an important boundary condition and is strongly related to the morphology of channels and tidal flats seaward of the sedimentation fields (Janssen-Stelder, in press 1). However, whether the sediment is deposited (when the net supply is positive) depends on the wave conditions within the sedimentation fields. The wave heights are greatly influenced by the height and maintenance of the brushwood groynes (Fig. 4.4).

4.3.2 The role of storm events in salt marsh development

During storm events, erosion of the pioneer zone and mudflat is dominated by wave activity. The currents are responsible for transporting the sediment once it is eroded. The correlation between the significant wave height and the net sediment flux is very good for the sites in the pioneer zone of the salt marshes. In case of the mudflat, the correlation is less good but still significant (Janssen-Stelder, in press 2). Storm periods have a similar effect on the pioneer zone at different locations along the salt marsh coast of the Dutch Wadden Sea.

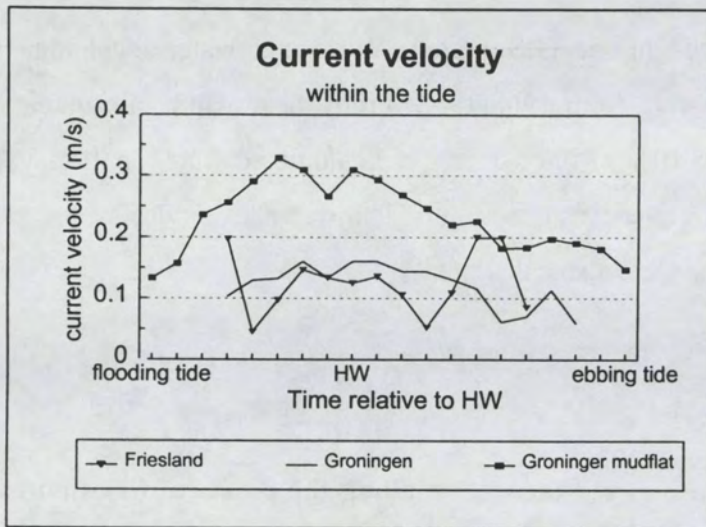


Fig. 4.5: Current velocity within the tide for salt marsh and mudflat locations.

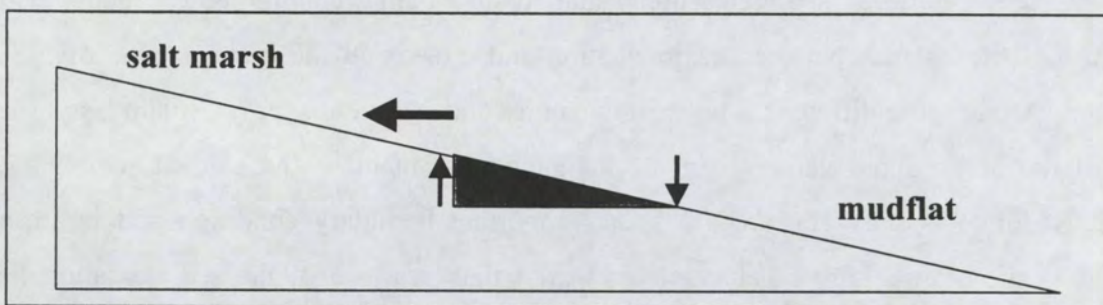


Fig. 4.6: Cliff erosion due to accretion difference on mud flat and salt marsh.

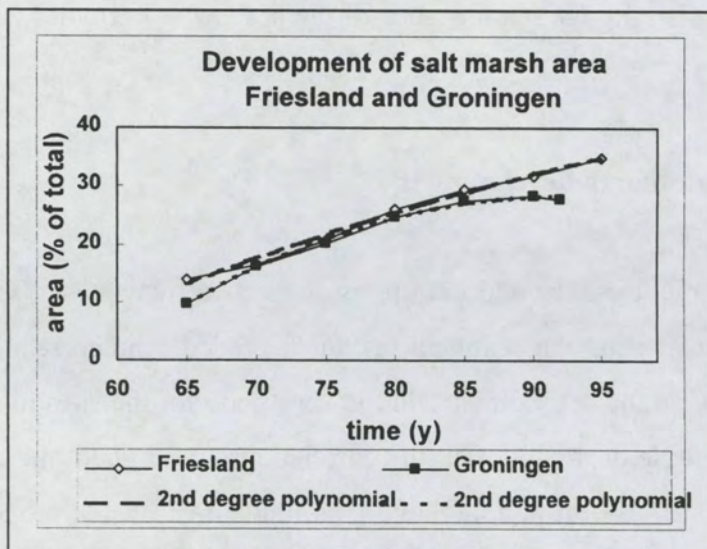


Fig. 4.7: Development of the Friesland and Groningen salt marsh areas between 1965 and 1995.

Wave heights, current velocity and suspended sediment concentrations showed the same values. Therefore the calculated bed shear stresses, sediment fluxes and transport rates agree.

During storm periods more sediment is eroded from the mudflat just seaward of the pioneer zone than in the pioneer zone itself. The main difference between the storm periods in the pioneer zones and the storm period on the mudflat was found in the current velocity, which average value was more than twice as high on the mudflat (Fig. 4.5). Therefore the calculated sediment fluxes and transport rates were larger on the mudflat during events.

The overall conclusion is that severe erosion takes place during storm periods once wave heights exceed 0.20 m. Erosion is greater on the mudflat in front of the pioneer zone of the salt marshes than in the pioneer zone itself. In the pioneer zone the currents are interrupted and slowed down by the brushwood groynes of the sedimentation fields whereas on the mudflat the current is not interrupted and reaches average values that are twice as high as in the pioneer zone.

A difference in transport capacity between the mudflat and pioneer zone is caused by this difference in current velocity and induces the difference in erosion between the mudflat and pioneer zone. This results in steepening of the coastal slope. During climatic changes, when wave action increases during increasing storm surges, waves will attack the steeper slope and the salt marsh will suffer from cliff erosion (Fig. 4.6).

4.3.3 Salt marsh development in the Dutch Wadden Sea from 1965 until present

This part of the study is based on long-term elevation data of the entire salt marsh coast of the mainland coast of the Dutch Wadden Sea. The data show that the salt marsh has been accreting since 1965. The accretion is almost linear for the Friesland part of the salt marshes. In the Groningen salt marshes the growth is asymptotic, it has stagnated since 1985 (Fig. 4.7, Janssen-Stelder, submitted).

The effects of wind and water level changes on the development of the total salt marsh area of the Friesland and Groningen coast were examined. The results showed that at a large time scale (decades), the Friesland salt marshes rapidly respond to changes in wind speed and high

water levels. The Groningen salt marshes slowly react to changes in wind speed and high water levels. An almost stable accretion balance is attained from 1965 until present in the Friesland salt marshes and therefore this area will better adjust to climatic changes, like increasing storm surge levels, than the Groningen salt marshes.

At a small time scale, the effect of one year with many storm days in combination with high water levels is similar for the Friesland and Groningen salt marshes. At the beginning of the storm year and in the year after the storm year erosion occurs and in the storm year accretion occurs. The salt marsh area is recovered two years after the storm year.

4.4 Discussion

This study has revealed the following issues with respect to climate change. Especially the combinations of sea level rise and an increase in storm frequency and duration effect salt marsh development. High wind speeds from a southwestern to northeastern direction induce a significant set up of the water level in the shallow Wadden Sea. The combination of high wind speeds and high water levels defines a storm surge. During a single storm surge there is a supply of sediment to the sedimentation fields of the salt marshes. On the other hand, erosion occurs on the mudflats located directly seaward of the salt marshes. This difference in accretion results in the development of a height difference between the mudflats and the pioneer zones of the salt marshes. Eventually this will lead to cliff erosion of the salt marsh.

At a larger time scale, an increase in storm surge level has a deteriorating effect on the salt marsh areas along the Friesland and Groningen mainland coast. The results of this study show that the salt marshes need a two-year recovery period after a year with a high storm surge level. When the storm surge frequency increases during climatic changes and high storm surge levels start to occur with an interval period smaller than two years, the salt marsh accretion will not recover from a year with high storm surge levels. The salt marsh accretion will decrease and eventually net erosion will occur. The salt marshes of the Groningen mainland coast attain a very delicate accretion balance at the moment, so these areas will suffer from erosion immediately. A decrease in accretion will occur in the salt marshes of the

Friesland mainland coast. If the sediment supply is sufficient this area may adjust to the climatic changes due to a more stable accretion balance.

The above stated relationships between storm surges and salt marsh development are useful for policy makers. Meteorological and water level data are continuously available for the Wadden Sea area. The salt marsh development can be predicted a few years ahead using these data and the above stated relationships. However, these relationships are only valid when the supply of sediment to the salt marsh areas is sufficient.

4.5 Conclusions and recommendations

Sediment supply and local wave action dominate in salt marsh development along the mainland coast of the Dutch Wadden Sea. During this study, relationships between sediment supply and morphology of the tidal flats and channels directly seaward of the salt marshes were discovered to be plausible. However, the exact relationships could not be proven significantly by the available data. Further research should focus on a holistic approach of the morphological development of the Wadden Sea, including the development of tidal flats, tidal channels and salt marshes.

This study also showed that local wave action determines whether the supplied sediment stays in suspension or is deposited within the sedimentation fields of the salt marshes. The height and maintenance of the brushwood groynes determines the wave action during calm weather condition. During storm surges, when the groynes are submerged, currents are still interrupted but the wave dampening effect reduces significantly. Further research should emphasize on ways to reduce wave action during storm surges in combination with additional supplies of sediment after storm surges.

At a larger time scale, an increase in storm surge level and frequency will seriously affect salt marsh development. This study showed that the salt marsh areas of the mainland coast of the Dutch Wadden Sea need a two-year period to recover from a year with many storm surges. At the moment the salt marshes along the coast of Friesland attain a positive accretion budget so the effect of an increase in storm surges will lead to a decrease in accretion. The salt marshes along the coast of Groningen show growth stagnation so the effect of an increase in storm

surges will directly lead to erosion in this area. Further research should focus on the difference between the development of the salt marshes in Friesland and Groningen so maybe a solution to prevent future rapid deterioration of the Groningen salt marshes can be found.

5 BIRD MIGRATION PROCESSES AND MODELLING: IMPROVING THE ECOWASP SHOREBIRD MODULE

5.1 Introduction

How will global climate change affect the many birds that depend on the Wadden Sea for their survival. This report describes the progress that has been made with answering this question during the second phase of the National Research Programme on Global Climate Change (NRP-II). During the first phase (NRP-I) the conceptual foundation of the current investigations and models was laid (Ens *et al.* 1995). During the second phase the models were further developed and scenario calculations could be performed in some cases. An important additional aim was to integrate the models with the ecosystem model of the Wadden Sea (EcoWasp).

The complexity of the problem derives from the fact that we deal with migratory birds. A typical example is the Knot *Calidris canutus*. Fig. 5.1 depicts the arctic breeding areas of the five distinct populations, their migration routes and their wintering areas. Two populations use the Wadden Sea. The *canutus* population passes through the Wadden Sea on migration to the African wintering grounds, while the *islandica* population spends the winter in the Wadden Sea and other estuaries along the coasts of Western Europe. Climate change may affect the birds in the breeding area, on migration and in the wintering area. For the time being, it is not possible to predict the combined effects of climate change in each of these areas. Instead, the annual cycle is broken into different stages and for each stage a model is built, starting from the choices of the individual birds. Next, population models are built that either combine the results of the sub-models, or depend for their justification on the insights generated by the models dealing with the choices of the individuals. Fig. 5.2 shows a simplified scheme and the fancy names given to the models to facilitate discussion.

DYNAMIG deals with the choices the birds have to make during migration (when to be where) and allows us to predict how habitat change will affect fitness components, like survival during migration and reproductive success on the breeding grounds.

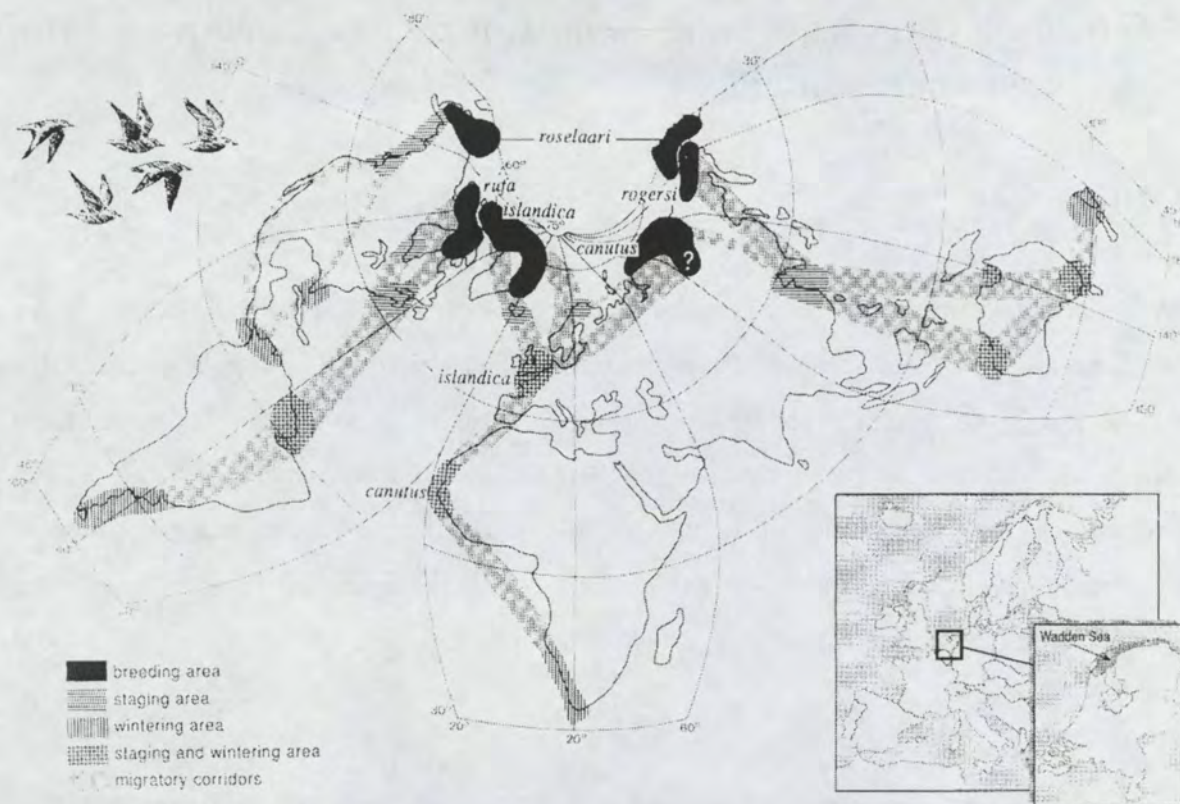


Figure 5.1: The worldwide distribution and the migration routes of the various subspecies of the Knot *Calidris canutus* (courtesy T. Piersma). The inset shows the Wadden Sea, which is important for two subspecies: *canutus* and *islandica*.

DEplete deals with the choices of the birds on the wintering grounds (where to feed), including interference during feeding and depletion of the food stock in the course of the winter. When it is known how climate change will affect the food stocks, it can be predicted how many birds will survive the winter under the new conditions.

LARGEPOP does not deal with choices of individuals, but describes the changes in the entire bird population as the result of processes on the wintering ground affecting mortality and processes on the breeding ground affecting reproduction (the migration period is considered to be part of the wintering stage).

HABITAT simply relates the density of birds to characteristics of the breeding, staging or wintering habitat and predicts changes in bird numbers from changes in habitat surface.

In the following we describe each of these models in more detail. Next we investigate for each model how habitat change, as a result of climate change will affect the birds. We end the chapter with a discussion on the most likely effects of climate change on the migratory birds depending on the Wadden Sea.

5.2 Materials and methods

This section describes the mathematical structure of the models in sufficient detail to allow a basic understanding. Detailed descriptions can be found in the various original publications on these models in the scientific literature (DYNAMIG: Weber *et al.* 1998 and Weber *et al.* 1999, DEplete: van der Meer & Ens 1997, LARGEPOP: Ebbinge *et al.* submitted, HABITAT: Brinkman & Ens 1998).

5.2.1 DYNAMIG

During migration the bird faces a series of strategic decisions. The ultimate goal is to maximise survival and reproduction. The important point is that the best decision at any one point in time depends on the outcome of previous decisions (Fig. 5.3). A full description of the model is provided by Weber *et al.* (1998), whereas Weber *et al.* (1999) use the model to study the effect of habitat change. The following is a summary of important parts of these two papers.

Basic outline

The environment consists of $i = 1, \dots, N$ linearly arranged sites, i.e. the wintering ground, $N-2$ stopover sites and the breeding site N . The distance between site i and $i + 1$ is denoted as D_i . The migration period is divided into $t = 0, \dots, T$ days. The state of a bird is characterised by its fuel stores x , measured as fuel load divided by lean body mass ($0 < x \leq x_{\max}$) and its location i . If stores fall to 0 the bird dies of starvation. Expected reproductive success depends on date of arrival and fuel load (eq. 5.1a). Reproductive success as a function of date of arrival may take two forms: reproductive success either (i) decreases monotonously, i.e. early arrival is always advantageous, or (ii) increases up to a maximum at an intermediate date and then decreases.

Behavioural options are either to forage with intensity u ($0 \leq u \leq 1$), or to fly to another site. Maximum net fuel gain g per unit time is deterministic. The foraging intensity u describes the fraction of the maximum fuel gain g that will be deposited per unit time. Risk of predation while foraging is only a function of foraging intensity (acquisition costs). Detailed

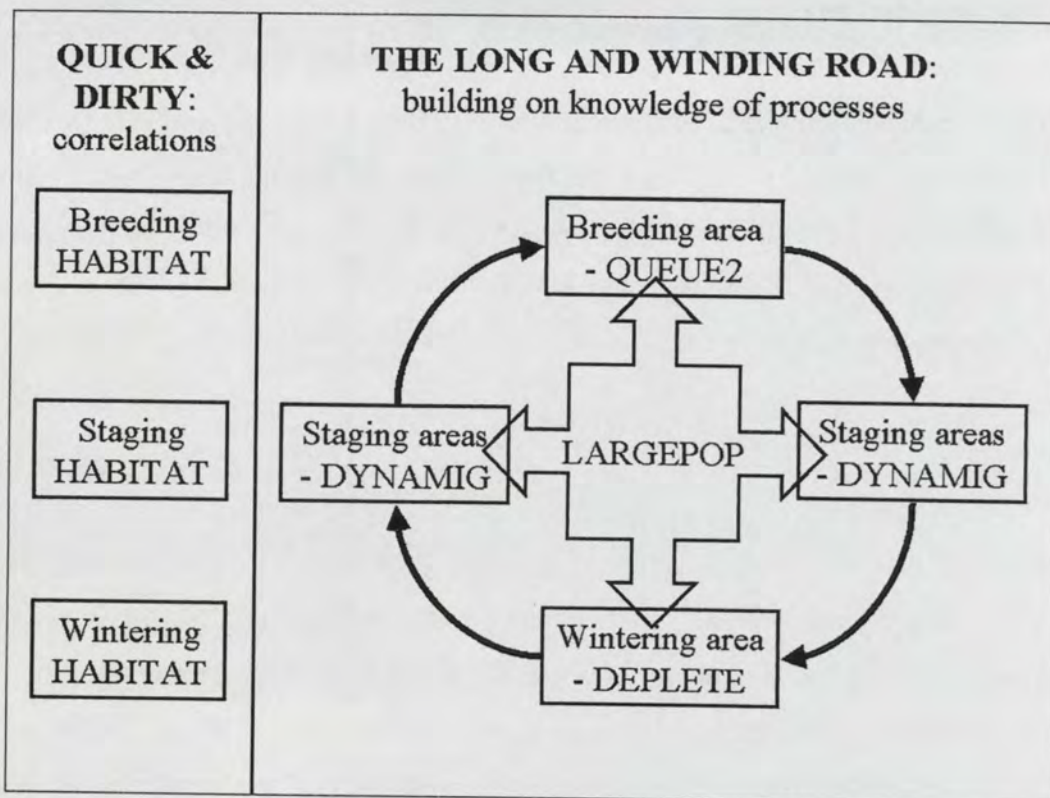


Figure 5.2: Scheme depicting how the various mathematical models relate to the annual cycle and to the modelling approach (correlational or building on knowledge of the underlying processes)

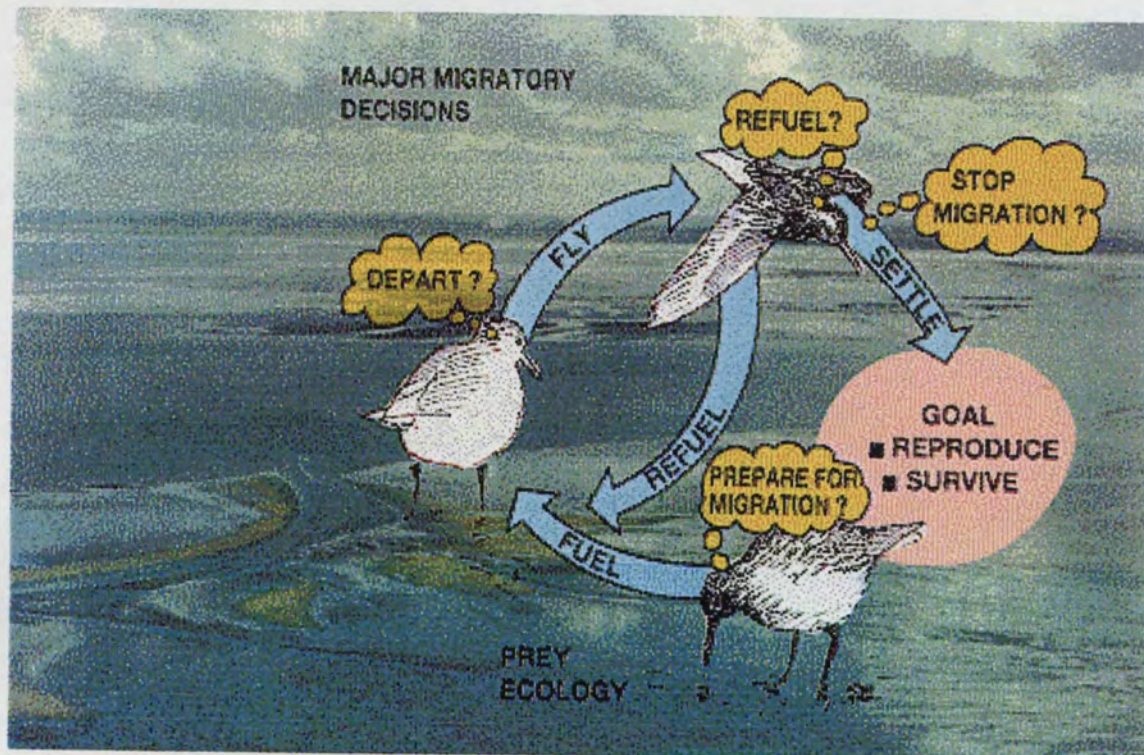


Figure 5.3: Scheme describing the important decisions that birds are facing during migration and the way these decisions are linked to each other (Ens *et al.* 1994).

justifications for the model assumptions and an analysis of other sources of predation risk are given elsewhere (Weber *et al.* 1998). The dynamic programming equations (see below) determine the optimal decision for all combinations of fuel stores, time and site. This decision matrix allows us to follow the fate of individual birds during their migratory journey using a Monte Carlo simulation (Mangel and Clark 1988): starting at site 1 each individual follows the policy defined by the decision matrix, which gives the optimal decision as a function of state and time. If results are derived analytically fuel loads and times are real-valued as opposed to integer-valued.

Parameter values used to study the effects of habitat loss in general

Habitat loss is modelled as a decrease in maximum fuelling rates. To simulate consequences of habitat loss we use two different scenarios: (i) changes occur on a time scale that allows birds to evolve the optimal policy for the new circumstances; (ii) birds use behavioural rules that result in sub-optimal behaviour in altered environments. We distinguish two forms of behavioural rules that lead to sub-optimal behaviour. First, the birds use behaviour that is optimal for a given energetic state, location and time as defined in the decision matrix but is not optimal for the current fuel gain. Second, they use a behaviour that only depends on the initial fuel load at $t = 0$ and is not at all responsive to the foraging conditions in the altered environment. For most of the cases considered below, this involves using a constant foraging intensity at all sites.

For distances, flight ranges and fuel gains, we have chosen parameter values that roughly conform to medium-sized waders like the Knot *Calidris canutus* and the Sanderling *Calidris alba* migrating along the East-Atlantic flyway to their Arctic breeding grounds. All parameters and their values are summarized in Table 5.1. If forward iterations are used to derive results, they are performed with a cohort of 50000 birds. The initial fuel load at $t = 0$ is 1 for all birds. The maximum fuel gain at sites i that are unaffected by habitat loss is $g(i) = 2$ and drops to 0.8 at the sites that are affected.

The dynamic programming equations

The expected future reproductive success of a bird with stores x at time t in location i that behaves optimally is denoted by $F(x, t, i)$. The expected future reproductive success $F(x, t, N)$ upon arrival at the final site N is:

$$F(x, t, N) = R(x)K(t) + B \quad \text{if } t \leq T \text{ and } 0 < x \leq x_{\max}. \quad (5.1a)$$

Table 5.1: List of model parameters (from Weber *et al.* 1999)

Parameter	Base-line value	Description
N	4	number of sites
D_i	2000 km	distance between site i and $i+1$ ($i < N$)
T	100	length of the migration period in days
t_{opt}	76 or 0	optimal arrival date at the breeding ground
B	0	expected future reproductive success
D	1.01 ($t_{\text{opt}}=76$) 0.0025 ($t_{\text{opt}}=0$)	rate of decrease of fitness at the breeding ground
x_{\max}	100	maximum fuel load
x_c	1	critical reserve level at the breeding ground required for reproduction
V	60 km/h	flight speed
$m_0(i)$	0	base-line mortality rate ($i < N$)
$m_y(i)$	$5 \cdot 10^{-4}$	attack rate for intensity-dependent predation risk ($i < N$)
B	2	exponent of intensity-dependent predation risk
C	14000 km	determines the flight range for a given fuel load
$g(i)$	2	maximum net fuel gain ($i < N$)

The first term on the right-hand side is the expected current reproductive success and B is the expected reproductive success from future breeding attempts. Birds that do not reach the breeding grounds in time only receive B , i.e. $F(x, T, i) = B$, $i < N$. The date-dependent function $K(t)$ takes the general form

$$K(t) = \begin{cases} \frac{t}{t_{\text{opt}}} & \text{if } t \leq t_{\text{opt}} \text{ and } t_{\text{opt}} > 0 \\ 1 - (t - t_{\text{opt}})d & \text{if } t > t_{\text{opt}} \end{cases} \quad (5.1b)$$

with $0 < t \leq T$ and $K(t) \geq 0$ for all t ; t_{opt} is the arrival date where $K(t)$ has a maximum and d is the rate at which $K(t)$ decreases after the optimal time. Either t_{opt} is in the interval $0 < t_{\text{opt}} \leq T$ such that birds could arrive before t_{opt} or $K(t)$ is a strictly monotonously decreasing function, i.e. $t_{\text{opt}} = 0$.

$R(x)$ is a unit step function:

$$R(x) = \begin{cases} 1 & \text{if } x \geq x_c \\ 0 & \text{if } x < x_c \end{cases} \quad (5.1c)$$

$x_c > 0$ is a minimum fuel load necessary for breeding.

Intensity-dependent predation per unit time (u) is an accelerating function of foraging intensity u :

$$\gamma(u) = m_\gamma(i)u^b, \quad i < N, \quad (5.2)$$

where $b > 1$ and $m(i)$ is a site specific constant attack rate.

The maximum expected future reproductive success $H_f(x, t, i)$ from foraging with the optimal intensity at any site $i < N$ at time t and gaining $g(i)$ and then following the optimal policy is:

$$H_f(x, t, i) = \max_u [(1 - \gamma(u))F(x + ug(i), t + 1, i)]. \quad (5.3)$$

Starting a flight with fuel load x_0 and flying distance D , the load x_a at arrival is (Weber *et al.* 1998)

$$x_a = \left(\frac{c^2}{(c - (Y(x_0) - D))^2} - 1 \right) 100, \quad (5.4)$$

where c is a constant measured in km (Pennycuick 1975); this equation is derived using the flight range equation by Alerstam and Lindström (1990, see also Weber and Houston 1997) Expected maximum future reproductive success when departing from site $i < N$ at time t and then following the optimal policy is:

$$H_d(x, t, i) = \max_j \left\{ F \left(x_a, t + \left(\sum_{l=i}^{j-1} D_l / 24v \right) j \right) \right\}, \quad i < j \leq N; \quad (5.5)$$

v is the flight speed in km per hour.

The optimal decision is the behavioural alternative yielding the highest future expected reproductive success:

$$F(x, t, i) = \max \{ H_f(x, t, i), H_d(x, t, i) \} \quad (5.6)$$

The terminal reward

In all the calculations, for both optimal and sub-optimal behaviour, we have used the terminal reward function that was defined for the unaltered environment. Using a new optimal policy or behaving according to previously optimal rules will, however, affect the reproductive

success in subsequent migratory episodes. This may become important if we want to estimate the consequences of habitat loss for population dynamics.

We can analyse the situation by assuming that the terminal reward consists of current and residual lifetime reproductive success. Lifetime reproductive success $V(x,t)$ is given by

$$V(x,t) = B(x,t)(1+n) \quad , \quad (5.7)$$

where $B(x,t)$ is the age-independent reproductive output as a function of state x and date of arrival t on the breeding ground and n is the expected number of future breeding attempts. The expected number of breeding attempts includes the mortality that is incurred during spring migration and is modelled above, but also all the mortality incurred in the rest of the annual cycle for which we provide no explicit model. The terminal reward as defined above is given by

$$\begin{aligned} F(x,t,N) &= V(x,t)/V(x,t_{opt}) \\ &= B(x,t)(1+n)/V(x,t_{opt}) \end{aligned} \quad (5.8)$$

where t_{opt} is the arrival date where $V(x,t)$ is at its maximum. Behaving according to rules that lead to sub-optimal behaviour results in all cases in a fixed delayed arrival at the breeding ground and an increased mortality. If birds behave optimally both arrival date and mortality can be affected. If the function $B(x,t)$ is not altered after habitat loss, the lifetime reproductive success $V'(x,t)$ in the new environment is

$$V'(x,t) = B(x,t)(1+n') \quad (5.9)$$

The expected number of breeding attempts n' now includes the increased mortality during the migratory episode and other possible consequences for the rest of the life-cycle. The terminal reward in the new environment is then given by

$$F'(x,t,N) = B(x,t)(1+n')/V(x,t_{opt}) \quad (5.10)$$

Comparing eqs. (5.8) and (5.10) shows that the terminal reward in the altered environment, $F'(x,t,N)$, is proportional to the terminal reward in the unaltered environment $F(x,t,N)$. Hence all our qualitative conclusions about the ranking of sites will not be affected by the assumption that the terminal reward is changed after the environment is altered.

Parameter values used to study the migration schedule of the Sanderling (*Calidris alba*)

To test if the dynamic migration model could be fitted to the migration schedules of migratory birds in the real world, we organised the international workshop DYNASHOP (Ens 1997, 1998). To this workshop we invited both modelers as well as field workers who had studied the migrations of a particular species in great detail. For each of these species we estimated the parameter values from existing data and we then investigated whether the model could help us understand peculiar aspects of the migration pattern of the species and what would happen when some parameters changed. Nine different species were investigated, but space only permits us to discuss one species, the Sanderling *Calidris alba*, in some detail. Thomas Weber, Gudmundur Gudmundsson and Peter Evans modeled this species.



Figure 5.4: Possible migration routes of Sanderlings (*Calidris alba*) spending the winter along the East coast of the United Kingdom (Teesmouth) and breeding in NE Greenland.

The migration patterns of Sanderling passing through Iceland in spring have been reviewed by Gudmundsson *et al.* (1991). They concluded that at least a quarter, but not all, of the northeast Greenland breeding population stop at one or other of two sites in SW Iceland. Some of these birds are known to winter at Teesmouth in N.E. England; others much further south on the eastern Atlantic coasts as far as Ghana. The spring passage through Britain involves stopover sites on both the east coast (including Teesmouth - Pienkowski and Evans 1984) and the west (Ferns 1979). Some birds using the west coast depart with body masses thought to be sufficient for a non-stop flight to Greenland.

The direct line of flight from Teesmouth to NE Greenland would lie to the north and east of Iceland (Fig. 5.4). The direct line of flight from Teesmouth to Iceland would pass over the Western Isles of Scotland (Hebrides), where several thousand Sanderling are known to stage

in most springs. None of the 400+ individually colour-ringed Sanderling from the Teesmouth wintering population has been seen in the Hebrides, however, although one has been seen in northwest Scotland.

Using the model of optimal migration strategies, the following questions were addressed:

- (1) "Should" Sanderlings from Teesmouth stage at the Hebrides on their way to Iceland? If so, under what conditions?
- (2) Under what circumstances should Sanderlings fly direct from Britain to NE Greenland, rather than making a dog-leg journey via Iceland and staging there if circumstances necessitate it?

For the first simulation, the parameters from Table 5.2 were used.

5.2.2 DEplete

This model deals with birds outside the breeding season, feeding on sessile prey items that do not reproduce during the study period. It describes for instance how a group of oystercatchers gradually deplete the stock of bivalves on which they feed in the course of one winter. It is assumed that the birds are ideal (i.e. they make decisions that maximise fitness and have perfect knowledge) and free (i.e. there are no costs of moving to other patches within the area). Their intake rate of food is positively related to food density and negatively to the density of conspecific competitors. First, we determine how the birds will distribute themselves over a given food supply. Next, we determine how the distribution of both predators and prey will change in the course of one winter. Van der Meer & Ens (1997) give a full description of the model.

Generalized functional response

In the equations that follow, upper-case letters usually denote variables, and lowercase letters parameters. Yet, we make an exception to this rule for those variables that refer to prey densities, predator densities, and patch areas. In those cases lowercase letters refer to a single patch, and upper-case letters to the entire system. For example, p_i ($\#/m^2$) is the predator

Table 5.2: List of parameter values used by Weber, Gudmundsson and Evans to study the migration schedule of the Sanderling during DYNASHOP.

Parameter	name in program	description	values
N	NSites	Number of staging sites	3 (Teemouth, Hebrides, SW Iceland)
T	FinalTime	number of time steps	70 days, from mid-April to 20 June, by which date most Sanderlings to choose to nest in NE Greenland have laid, or 55 days, resulting from an inability to begin fattening before 1 May, or from an advance in the optimal breeding date in the arctic due to climate warming
x_{\max}	Cap		100
	NGains	number of possible gain levels at site	3
	w	determining shape of state dependent fitness function	<10% poor
x_c	xc	determining shape of state dependent fitness function	1
	sigm	0: step fit func at $x=1$, 1:w & xc determine	0
Di	Y	distance between sites	Teemouth to Hebrides 500 km Hebrides to Iceland 1150 km SW Iceland to NE Greenland 1450 km Teemouth to NE Greenland 2600 km
C	c	flight range parameter (km)	11400
V	speed	flight speed (km/day)	1200 km/day
m_0I	b0	predation risks at sites: baseline mortality	2.5×10^{-4} per day
$m_y(i)_p(i)$	b1	predation risks at sites: coefficient	10^{-7}
A	a	predation risk: mass dependent exponent	2
B	g	predation risk: intensity dependence exponent	0
t_{opt}	topt	optimal arrival time at breeding ground	50-69
D	slopefit	rate of decrease fitness at breeding site	up to day 49: fitness 0 ; day 50-69: fitness 1 arrival after day 70: fitness 0
$g_j(i)$	Gains	site 1 gain levels site 2 gain levels site 3 gain levels	Teemouth 1.0 g/day Hebrides 1.5 g/day Iceland 3.0 g/day
$p_j(i)$	GainsProb	site 1 gain probability site 2 gain probability site 3 gain probability	0 1 0 0 1 0 0 1 0
	ex	expenditure at the sites	0 0 0
	NWind	number of wind classes	5
δ_k	WindAssist	wind assistance	-0.5 -0.25 0 0.25 0.5
q_k	WindProb	probability distribution of wind assistance	during May for Teemouth to Iceland 0.18 0.40 0.30 0.10 0.02 for Teemouth - Greenland 0.15 0.30 0.20 0.30 0.15
B	B	expected future reproductive success	0.5

density in patch i , whereas P ($\#/m^2$) is the overall predator density, that is the total number of predators in the system divided by the total area. For the sake of convenience, it is assumed that prey items are of equal size, require equal handling time, and are captured and eaten upon discovery. Unless stated otherwise, predators are always foraging. While foraging, they are either searching, handling, or (in some cases) “fighting”. We distinguish searching rate A (m^2/s), which is the area searched per predator per unit searching time, encounter rate E ($\#/s$), which is the number of prey items encountered per predator per unit searching time, and intake rate W ($\#/s$), which is the number of prey items eaten per predator per unit foraging time, i.e. including handling and fighting time.

Generally, the intake rate per unit foraging time per predator in patch i , W_i ($\#/s$) is given by a function of prey density n_i ($\#/m^2$) and predator density p_i ($\#/m^2$)

$$W_i = f(n_i, p_i) \quad (5.11).$$

Usually, the intake rate W increases with increasing prey density n and decreases with increasing predator density. “Ideal” and “free” predators will distribute themselves between patches such that none can improve their intake rate by moving to another patch. Providing that individuals are identical, this means that intake rate is equal across patches. Hence for all patches $i = 1, 2, \dots, I$ (assuming for the time being that they are all occupied)

$$W_i = f(n_i, p_i) = c \quad (5.12).$$

Below we will for various functions f derive the function g that relates predator density to prey density, the so-called aggregative response:

$$p_i = g(n_i, c) \quad (5.13)$$

for all patches. Given the frequency distribution of habitats in terms of surface area d_i and prey density n_i , the spatial distribution of predators (the “ideal free distribution”) is determined by this aggregative response function. The constant c is determined by the constraint

$$\sum_{i=1}^I d_i p_i = DP \quad (5.14)$$

where $D = \sum_{i=1}^I d_i$ (m^2) is the total surface area of all patches, and DP (#) is the total number of predators in the system. If possible an explicit equation for c will be given. All model parameters are (unless otherwise stated) assumed to be greater than zero.

Deriving the shape of the aggregative response

Two basic approaches exist to estimate the parameters dealing with interference, i.e. the decrease in intake rate due to an increase in the density of conspecifics feeding in the same patch. The mechanistic approach makes assumptions on the mechanism of interaction between the birds and then works out the parameters from these assumptions on the interference process. The phenomenological approach uses empirical studies to estimate the shape of the interference function. Different regression models have been used, leading to different functions. Below, we will only derive results for the models based on the mechanistic approach as these are conceptually more satisfying than the models based on the phenomenological approach. However, at the end of the paragraph we present a table summarizing the main conclusions for all models.

Ruxton *et al.* (1992) made several simple behavioural models of the predation process by using an approach borrowed from chemical reaction kinetics. The predator population is divided in several mutually exclusive states. Given the transition rules between the states, the functional response follows from the steady-state solution of the accompanying differential equations. For example, if a searching and a handling state are distinguished, each transition from handling back to searching is supposed to mean that a prey item is swallowed. Hence the transition rate at the steady-state yields the functional response. It is interesting to note that this simple example leads to Holling's disc equation (Holling 1959), and the intake rate can be written as:

$$W_i = \frac{an_i}{1 + ahn_i} \quad (5.15)$$

where a is the constant searching rate (m^2/s), and h is the handling time (s). Yet, since interference does not occur (there is no fighting state in which individuals are involved in encounters with conspecifics) and intake rate therefore does not depend on predator density, it

is not possible to derive the aggregative response function: all “ideal” and “free” animals will aggregate in the patch with the highest prey density. The relation between intake rate and prey density as given in eq. (5.15) is also known as the type II functional response. Contrary, a type I functional response refers to the situation where the intake rate is proportional to prey density. This can be regarded as a special case of the type II functional response when the handling time h equals zero.

In the more complex models that Ruxton *et al.* (1992) examined, an encounter between predators could mean that a (searching or handling) predator stops its pursuits and enters the “fighting” state. They showed that if a searching predator interacts with both searching and handling individuals, the functional response can be approximated by Beddington’s (1975) equation:

$$W_i = \frac{an_i}{1 + ahn_i + qp_i} \quad (5.16)$$

where q is a parameter which is actually twice the product of the “rate of predator discovery” (m^2/s) times the “loss of searching time per encounter” (s). As these two parameters always occur together, they can be replaced by the compound parameter q (m^2), which may be called the interference area. If a searching predator may also interact with a predator already involved in an aggressive encounter, the same model arises, but with a slightly different interpretation of the parameter q .

Setting the intake rate equal for all patches i

$$\frac{an_i}{1 + ahn_i + qp_i} = c \quad (5.17)$$

leads after some straightforward algebraic manipulation to a linear relationship between predator density p_i and prey density n_i

$$p_i = -\frac{1}{q} + \frac{a(1/c - h)}{q} n_i \quad (5.18)$$

For patches with a prey density $n_i < \frac{1}{a(1/c - h)}$ predator densities are set equal to zero, as negative predator densities are nonsense. For the same reason, $1/c$ (which is the average foraging time per prey item consumed and thus includes handling time) must always be larger than the handling time h . This constraint holds for all models that follow.

Now assume that the first $j - 1$ patches (the I patches are ordered in increasing prey density) remain unoccupied with predators. Then the value for the constant c can be derived from

noticing that the total number of birds in the system, which is known, equals $D^*P^* = \sum_{i=j}^I d_i p_i$,

where $D^* = \sum_{i=j}^I d_i$ is the total surface area (m^2) of all occupied patches, and P^* is the overall

predator density ($\#/\text{m}^2$) for all occupied patches. Similarly, $D^*N^* = \sum_{i=j}^I d_i n_i$, where N^* is the overall prey density ($\#/\text{m}^2$) for all occupied patches. Then,

$$P^* = \sum_{i=j}^I \frac{d_i}{D^*} p_i = \sum_{i=j}^I \frac{d_i (a(1/c - h)n_i - 1)}{D^* q} \quad (5.19)$$

which results in

$$c = \frac{aN^*}{1 + ahN^* + qP^*} \quad (5.20)$$

The value of j can be derived from noticing that the birds should not visit those patches for which the intake rate without considering interference is smaller than the intake rate (taking interference into account) would be, if only the plots that have a higher prey density are visited. Thus, the patch $j - 1$ (recall that patches are ordered in increasing prey density) for which

$$\frac{an_{j-1}}{1 + ahn_{j-1}} < \frac{aN^*}{1 + ahN^* + qP^*} \quad (5.21)$$

holds, remains empty with predators. The same is true for all patches with even lower prey densities. Below we will refer to this model, in which searching predators interact with both searching and handling conspecifics, as the Beddington model.

Ruxton *et al.* (1992) also showed that if a searching predator only interacts with other searching predators, the functional response approximately looks like:

$$W_i = \frac{an_i}{1 + ahn_i + \frac{qP_i}{1 + ahn_i}} \quad (5.22)$$

Proceeding as above,

$$p_i = -\frac{1}{q} + \frac{a(1/c - 2h)}{q}n_i + \frac{a^2h(1/c - h)}{q}n_i^2 \quad (5.23)$$

and

$$c = \frac{aN^* + a^2h \frac{\sum_{i=j}^I d_i n_i^2}{D^*}}{1 + 2ahN^* + a^2h^2 \frac{\sum_{i=j}^I d_i n_i^2}{D^*} + qP^*} \quad (5.24)$$

In spite of its complexity, the occurrence of the term $\sum d_i n_i^2$ in the latter equation tells us that the intake rate c depends on the variance of the prey densities in the suitable patches $i = j, j+1, \dots, I$. In contrast, the Beddington model predicted an intake rate (eq. 5.20) that only depends on the overall prey density N^* in the suitable patches. Below we refer to the “search-interaction-only” model as the Ruxton model. In the trivial case when the handling time is zero, the two models are equivalent.

The aggregative responses resulting from the various interference models are compared in Table 5.3.

Table 5.3: A characterisation of the interference models. The last column shows whether the second derivative of the aggregative response function is positive, zero or negative for all prey densities greater than zero (provided that the searching rate, handling time and interference coefficient are greater than zero). The $\text{sign}(x)$ function gives the sign of x , thus if $x > 0$ then $\text{sign}(x)$ should be read as $+$. From van der Meer & Ens (1997).

Model	Effect on	Threshold prey density	Maximum predator density	Second derivative
Beddington	searching and handling	$\frac{1}{a(1/c - h)}$		0
Ruxton	searching	$\frac{1}{a(1/c - h)}$		+
Hassell-Varley	searching rate			$\text{sign}\left(\frac{1}{m} - 1\right)$
Doublelog	intake rate		$r\left(\frac{1}{ch}\right)^{1/m}$	-
Semilog	intake rate		$r \exp\left(\frac{1 - ch}{m}\right)$	-
Untransformed	intake rate	$\frac{1}{a(1/c - h)}$	$\frac{1 - ch}{q}$	-

Prey depletion in the course of one winter

The aggregative responses that we calculated only apply to a single moment in time. However, due to predation prey will be depleted. If there is no concurrent prey renewal, as is the case for waders that feed on benthic invertebrates in winter, this means that the standing stocks of prey in the occupied patches continually decline. Under the ideal free assumption, this may lead to a redistribution of the predators. We are not able to provide analytical solutions for this process of redistribution under depletion, but a look at the shape of the aggregative response points to some generalisations. First, for those aggregative responses that are characterised by a threshold density, it is clear that this threshold prey density will shift downwards as depletion proceeds, i.e. poorer and poorer patches will be occupied. Second, for those models (Hassell-Varley, Ruxton) where predators strongly aggregate in the best patches, these patches will be severely depleted and the predators will subsequently spread out to patches of lower quality, i.e. patches will quickly become more similar in the course of winter. In contrast, if there is a maximum predator density, as in the models that were based on the empirical relationship between intake rate and predator density, it could be

Table 5.4: Parameter values used for various possible descriptions of the generalized functional response.

Model	Parameter	units	value
all models	Maximum search rate	m ² /s	0,0007
all models	Handling per prey	s	50
all models	Minimum intake rate	prey/s	0,002
all models	Normal intake rate	prey/s	0,0021
Beddington	Interference area q	m ²	1000
Ruxton	Interference area q	m ²	1000
Hassell-Varley	Interference factor m	-	0,4
Hassell-Varley	Reference density r	#/m ²	0,0001
Doublelog	Interference factor m	-	0,27
Semilog	Reference density r	#/m ²	0,0001
Untransformed	Interference area q	m ²	20

Table 5.5: Description of the Dutch Wadden Sea. Habitat types are distinguished on the basis of emersion time. The prey density refers to “standardised” shellfish of 0.25 gram AFDM, available to oystercatchers, making up 50% of the total biomass of benthic animals. The table refers to an average year.

habitat type	Surface (km ²) current situation	surface (km ²) after 60 cm sea level rise	height (m)	emersion period (fraction time)	prey density (#/m ²)
1	184	159	0,14	0,06	12
2	197	168	0,45	0,16	36
3	183	156	0,77	0,25	72
4	163	110	1,05	0,34	60
5	162	64	1,33	0,42	48
6	157	48	1,65	0,52	36
7	77	27	1,94	0,64	24
8	123	23	2,38	0,85	6

that a good patch is effectively underused relative to a poor patch so that depletion in terms of the fraction of prey removed will be more intense in the poor patch.

We will examine these suggestions by numerical simulations. We will show the effect of prey depletion in the course of the winter on changes in the aggregative response of the Oystercatcher. In our approach, each day (the winter starts at September 1 and ends at day 215, i.e. March 31) the birds are redistributed over all patches according to the various aggregative response functions. In order to survive, the birds have to balance their energy budget. This requirement implies that they have to gather a more or less fixed amount of food each day. Extra food intake will not increase their fitness, as they can not direct it into growth or reproduction. Thus, the predator-prey system is of a relatively simple structure. Prey decreases at a rate determined by the number of predators in the system times the fixed rate of food intake per predator. Predators either survive or die. They die when their intake rate gets consistently below their energy requirements. Yet in the numerical example presented here this did not occur. Each day prey density n_i in each patch decreases by the bird density p_i times the required intake rate c_0 (#/s) times the day length (s). Model runs are performed for oystercatchers feeding on bivalves of 0.25 g ash-free dry mass. The required intake rate c_0 is based on a power of 8.8 W, which is the estimate for a winter day with a temperature of about 5 °C (Kersten & Piersma 1987). These energy needs correspond to a digestion efficiency of 0.8 (-) times energy content of 22000 (J/g) times a daily averaged ash-free dry mass intake rate of 0.0005 (g/s). This implies a daily food intake of 0.0005 (g/s) times 86400 (s) is 43.2 g/day or 173 #/day. If a day contains 12 hours foraging time the required intake rate while foraging is 0.001 g/s or 0.004 #/s, that is one prey every 250 s. The parameters used for the generalized functional response are given in Table 5.4. The initial prey densities, and the patch areas are given in Table 5.5.

5.2.3 LARGEPOP

Complex simulation models exist to describe the population dynamics of an entire bird population. We had two aims with LARGEPOP. First, to develop a model that was sufficiently simple to be analytically tractable. Two, to develop a model for which the

parameters could be estimated from existing data. A paper with a full description has been sent to a scientific journal (Ebbinge *et al.* submitted).

LARGEPOP is a discrete time mathematical model which divides a year into two seasons: a reproductive and a non-reproductive season (akin to models in Fretwell, 1972, and Goss-Custard & Sutherland, 1997). We assume that in the reproductive season there is no mortality. In our model we had to simplify the real world in order to be able to use the existing population data, which are based on annual censuses in mid-January. In the model therefore the population size just after reproduction in August is estimated, by including only those newly born geese that eventually manage to survive till January. Thus, part of the mortality of young-of-the-year is included in the estimated reproduction. Therefore our reproductive season runs from January till August, and the non-reproductive season from August till January. In the model all mortality only occurs during this non-reproductive season. In this way all mortality in the model is concentrated during the period of autumn migration, which realistically coincides with the hunting season. We count years starting just after the breeding season and let k denote the year, $k = 0, 1, \dots$, where 0 corresponds to 1955. We differentiate between two seasons in the same year and we want to express this in the notation. By N_{2k} we denote the population size of Dark-bellied Brent Geese in August of year k , and discount all young that are doomed to die before January. By N_{2k+1} we denote the population size after the autumn migration in January of the next year. So, for example, year 0 has the population sizes N_0 just after the breeding season in 1955 and a population size reduced by mortality N_1 at the start of the wintering season in 1955-56). Likewise N_3 denotes the population size just after the breeding season in year 1 (1956) and N_4 the winter population in 1956-57, etc.

We assume that the number of first-winter birds in year k , is given by

$$N_{2k-1} f(N_{2k-1}) \quad (5.25)$$

where f is a function that describes the possible density dependence in reproductive success (i.e. any density dependence is assumed to arise from the numbers of birds present in the breeding season). Similarly, we assume that the number of birds that do not survive the autumn season in year k is given by

$$N_{2k} h(N_{2k}) \quad (5.26)$$

where $h(N_{2k})$ is the fraction of birds that does not survive the non-reproductive season, which could possibly be density dependent. In the next section we estimate both $f(N)$ and $h(N)$ as functions of N from the data.

Our basic model becomes

$$\begin{aligned} N_{2k} &= N_{2k-1}(1 + f(N_{2k-1})) \\ N_{2k+1} &= N_{2k}(1 - h(N_{2k})). \end{aligned} \quad (5.27)$$

We analyze the following model:

$$\begin{aligned} N_{2k} &= N_{2k-1}(1 + (a + bN_{2k-1})e^{-cN_{2k-1}}) \\ N_{2k+1} &= N_{2k}(1 - \delta) \end{aligned} \quad (5.28)$$

Since the time-unit of one year has been cut into two half-year seasons, we look for steady state pairs (N, M) such that

$$\begin{aligned} N &= M(1 + (a + bM)e^{-cM}) \\ M &= N(1 - \delta) \end{aligned} \quad (5.29)$$

(i.e. a steady state is a pair (N, M) such that in each consecutive year there will be N of birds at the start of the summer season and M birds at the start of the winter season). One can immediately see from the second equation that $M = N(1 - \delta)$. We can then find N by solving

$$N = N(1 - \delta) + (a(1 - \delta)N + b(1 - \delta)^2 N^2)e^{-c(1 - \delta)N} \quad (5.30)$$

This leads to $N = 0$, or, for positive N , the possible solution of

$$\frac{\delta}{1 - \delta} = (a + b(1 - \delta)N)e^{-cN(1 - \delta)}. \quad (5.31)$$

We cannot solve the latter equality for N analytically, but we can analyse it graphically by plotting the right-hand side, which we denote by $g(N) = f(N(1 - \delta))$, and the left-hand side, a horizontal line, in one graph as functions of N . The behaviour of g as a function of N is straightforward, it is unimodal; at $N = 0$, we have

$$g(0) = a \quad (5.32)$$

and its derivative is given by

$$\frac{d}{dN} g(N) = -c(1-\delta)(a + bN(1-\delta))e^{-cN(1-\delta)} + bN(1-\delta)e^{-cN(1-\delta)}. \quad (5.33)$$

The function g has a maximum at

$$\bar{N} = \frac{b - ca}{cb(1-\delta)}. \quad (5.34)$$

The intersection points N^* correspond to steady state pairs $(N^*, N^*(1 - \delta))$ of our system. We study the various possibilities for intersections of the curves as we vary the only parameter with a clear biological interpretation, i.e. δ , the per capita probability of not surviving the winter season. The other parameters (a, b, c) are set to the values estimated for them from the reproduction data. The bifurcation diagram (Fig. 5.5) is a numerical calculation of the steady

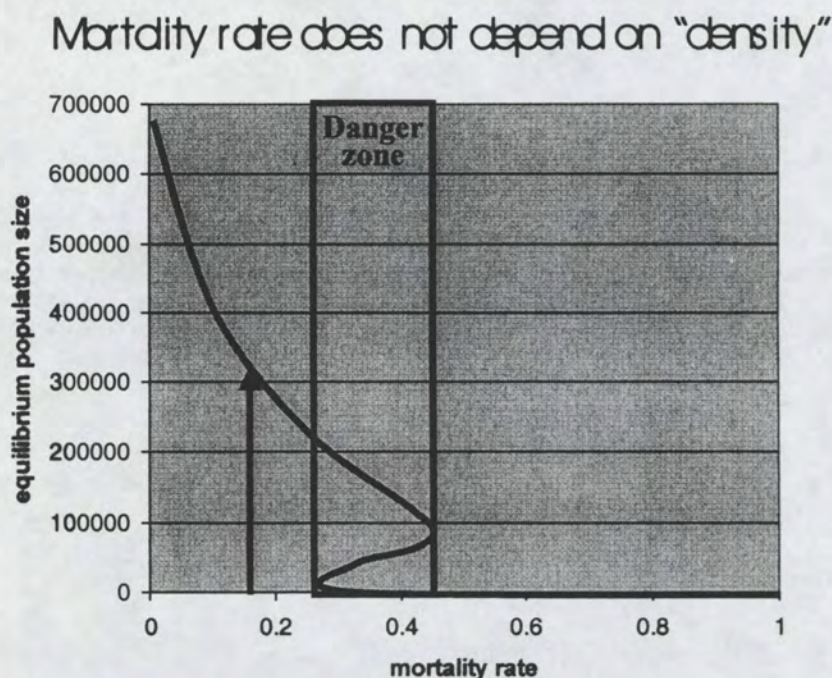


Figure 5.5: Bifurcation diagram where the steady state population size N^* , as calculated from the model, is given as a function of the model parameter δ , the per capita death rate. The graph has two branches. The horizontal branch at $N^*=0$ corresponds to the zero steady state, which exists for all values of δ . This state is unstable to the left of the dot and stable to the right of the dot. The curved branch corresponds to a positive steady state. This state is stable everywhere, except for the backward branching part in between the two dots. From Ebbinge *et al.* (submitted).

state value for N as a function of the parameter δ . We can fully understand the dynamics of the model, and the graph in Fig. 5.5, by the following argument. The unimodal curve $g(N)$ can have no intersection, one intersection or two intersections with the horizontal line $N = \delta/(1-\delta)$. If we increase δ from slightly larger than 0 to slightly less than 1, the horizontal line will shift upward. The unimodal curve will change as well, but will stay unimodal. The different possibilities for the resulting intersections correspond to regions for δ where $N^* = 0$ is the only steady state (and stable), where there is one positive stable steady state, and where there are two positive steady states, one stable and one unstable.

A straightforward calculation allows us to obtain the regions in the interval $0 < \delta < 1$ with the appropriate behaviour. If $\delta/(1-\delta) < a$, there is only one positive intersection, i.e. if $\delta < 0.32$ (approx.). If $\delta/(1-\delta) > a$, there are two positive intersections, until the horizontal line reaches the top of g (where the two intersections merge). This point can be obtained by solving

$$g(\bar{N}) = \frac{\delta}{1-\delta} \quad (5.35)$$

for δ . This has an explicit unique solution $\delta \approx 0.44$. If δ is increased further we see that the curves no longer intersect and 0 is the only steady state. The steady state 0 is stable for the whole region characterised by $\delta/(1-\delta) > a$.

5.2.4 HABITAT

In stark contrast to the previous models, which seek to derive important relationships from an understanding of the underlying processes, the HABITAT model simply correlates the densities of birds to properties of the habitats in which they live. This can be done for each stage of the annual cycle of the bird. To date we have only developed the model for waders feeding on intertidal mudflats of the Wadden Sea during the non-breeding season, in particular during late summer and early autumn, when numbers are maximal. Brinkman & Ens (1998) provide a full description.

The feeding density of the birds (D in numbers per m^2) is predicted from the median grain size of fractions greater than 16 μm (M in μm) and emersion time (E in hours) as follows:

Table 5.6: Comparison of predicted total number of birds feeding on intertidal mudflats in the Dutch Wadden Sea during July-Sept with the numbers actually counted (N=8) in the period 1979-1990. For each species the following data are listed: the minimum number, the maximum number, the mean number, the standard deviation (SD), the standard deviation as % of the mean (RSD), whether a good habitat model could be fitted, the number predicted and the predicted number as percentage of the mean counted. From Oost *et al.* (1998).

Species	min	max	mean	SD	RSD	fit	pred.	ratio
Curlew Sandpiper	102	1465	795	478	60%	no fit		
Spotted Redshank	914	3130	2006	837	42%		1037	52%
Ringed Plover	888	4752	2114	1199	57%		1287	61%
Turnstone	1225	3870	2257	813	36%	no fit		
Greenshank	1292	4309	2500	1178	47%		1696	68%
Avocet	8308	17554	12790	2895	23%	no fit		
Redshank	12306	31332	18366	6516	35%		43244	235%
Grey Plover	11650	33240	20864	7536	36%		19119	92%
Shelduck	2677	37515	26664	11857	44%	no fit		
Common Gull	18207	43902	29190	9162	31%	no fit		
Bar-tailed Godwit	28152	57655	36687	10530	29%		42278	115%
Knot	29937	52648	42049	8790	21%		5400	13%
Black-headed Gull	43677	98335	72308	20054	28%		340000	470%
Herring Gull	33961	114499	76392	32232	42%		17500	23%
Curlew	44265	138005	91867	26366	29%		65037	71%
Dunlin	119434	375300	187454	81163	43%		19300	10%
Oystercatcher	161485	272818	223671	39181	18%		126268	56%

$$D = \exp(a + bM + cM^2 + dE + eE^2 + fME) \quad (5.36)$$

where a , b , c , d , e and f are constants. When $f=0$, this equation yields a Gaussian distribution with contours in the shape of ellipses whose main axes are parallel to the M-axis and the E-axis. When f does not equal 0, the effects of grain size and emersion time are not independent of each other. As a result of this interaction, the two main axes of the contour ellipses will not be parallel to the M-axis and the E-axis.

The constants must be fitted from the data using statistical procedures. We employed a Linear Modelling Technique from the Genstat statistical package, using a least-squares criterion. A problem with the available data set was that we had no observations of sandy flats with a long exposure period. Such areas are known to hold few birds, so we decided to include zero values. Even then it was not always possible to obtain meaningful parameter estimates. When this happened, we have indicated this with *no fit* in Table 5.6. For species where we succeeded in obtaining a meaningful model, we used it to predict the total number of individuals for the entire Dutch Wadden Sea. In some cases there was a large discrepancy between predictions and observations, especially in rare species. However, in a surprising number of species the predicted number was reasonably close to the observed number and for these species we felt confident that we could predict the effects of habitat change.

5.3 Results

Effects of climate change on the Wadden Sea

The various bird models that we discuss in this chapter relate bird numbers or bird behaviour to habitat change. Thus, if we want to predict the effects of climate change, we must first investigate how climate change will affect the habitats on which the birds depend. Precise scenarios are only available for the Wadden Sea, as this was the target area for this NRP project. These scenarios only apply to the effects of sea level rise, i.e. the effects of a rise in temperature are ignored. Both DYNAMIG and LARGEPOP require knowledge on all areas along the migration route. Thus, these Wadden Sea scenarios can only be used for calculations with DEplete and HABITAT, which can be applied to the Wadden Sea without knowledge on habitat change elsewhere along the migration route.

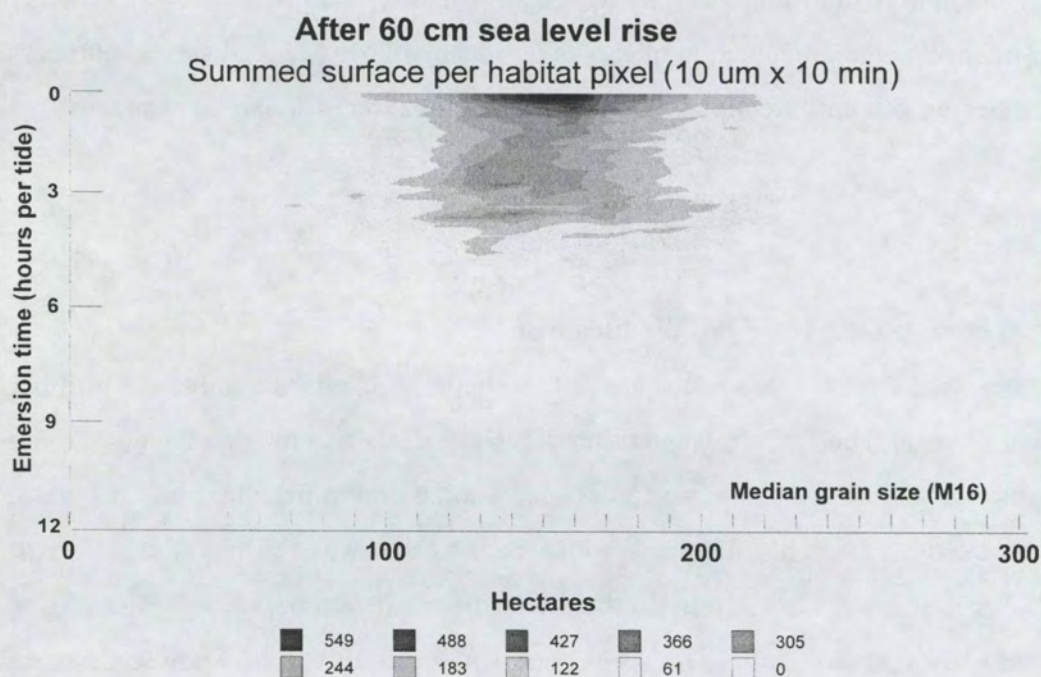
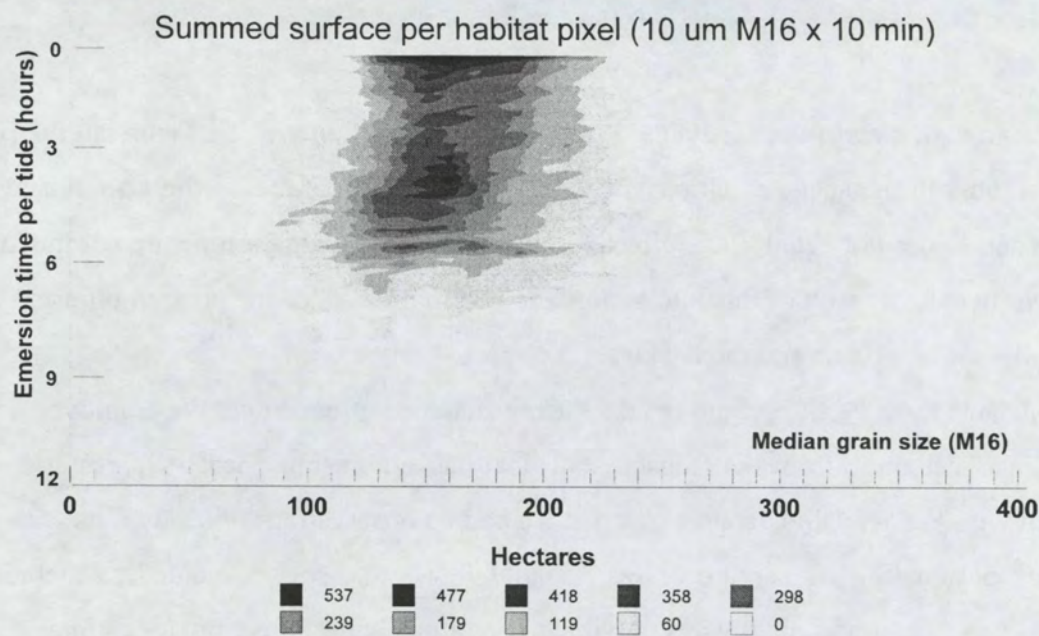


Figure 5.6 a,b: Characterisation of the intertidal habitats in the Dutch Wadden Sea according to emersion time and median grain size for (a) current situation, (b) after 60 cm sea level rise without compensation through sedimentation. From Brinkman & Ens (1998).

For the HABITAT model we need to characterise the Wadden Sea according to emersion time and sediment. It turns out that in the current Wadden Sea there are hardly any flats, which are exposed longer than 6 hours per tidal cycle, while the median grain size (M16) varies between 120 and 200 μm (Fig. 5.6a). On average, areas that are high in the tidal zone are exposed longer and have softer sediments, i.e. with smaller grain size. However, perhaps rather surprisingly, this relationship between emersion time and median grain size is not very strong in the current Wadden Sea. To simulate the effect of sea level rise, an extra amount of water is added and it was calculated how this would affect emersion time in each habitat. We ignored the possibility that the sediment characteristics would be affected as well. Thus, it comes as no surprise that the primary difference between the habitats in the Wadden Sea before and after a 60 cm sea level rise is a strong decrease in the areas with a relatively long emersion time (Fig. 5.6b). The maximum sea level rise that was simulated in this way was 120 cm.

To apply DEplete, we need to characterize the Wadden Sea according to the food supply for the birds, i.e. Oystercatchers. This food supply consists of benthic animals living on and in the sediment. For the calculations it was assumed that the food supply was primarily determined by the emersion time, i.e. the effect of grain size was ignored. Table 5.5 shows the density of standardized prey animals weighing 250 gram AFDM for the different habitats. Because of our assumption that prey density is only determined by emersion time, we can indicate the effect of sea level rise in the same table. Especially the surface of habitats with a long emersion time will decrease strongly following a 60 cm increase in sea level that is not compensated by sedimentation.

5.3.1 DYNAMIG

The migration pattern of the Sanderling

As described previously, we chose the Sanderling to exemplify the results of DYNASHOP, the international workshop on dynamic models of migration. Simulation 1 predicted that the birds should use the stopover site in the Hebrides. However, it turned out to be unrealistic as it predicted that all Sanderlings should leave Teesmouth by 1 May and fly to the Hebrides (Fig. 5.7a). Most Sanderling do not leave Teesmouth until at least 2 weeks later. Also it predicts that the departure state from Teesmouth involves fat levels of about 1 % of the lean

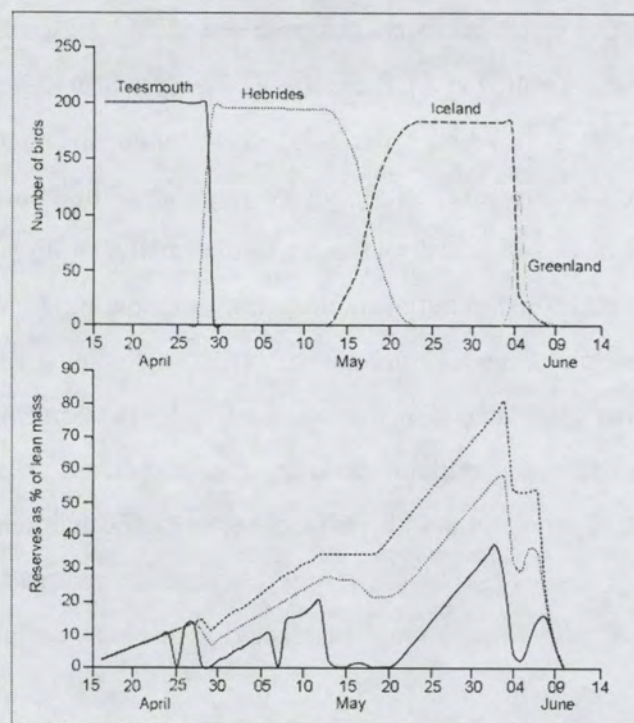


Figure 5.7: Results of simulation 1 by Weber, Gudmundsson and Evans for the Sanderling. (a) Predicted pattern of site use. (b) Predicted pattern of mass gain.

Oystercatchers Dutch Wadden Sea DEPLETE: average food supply & Beddington interference

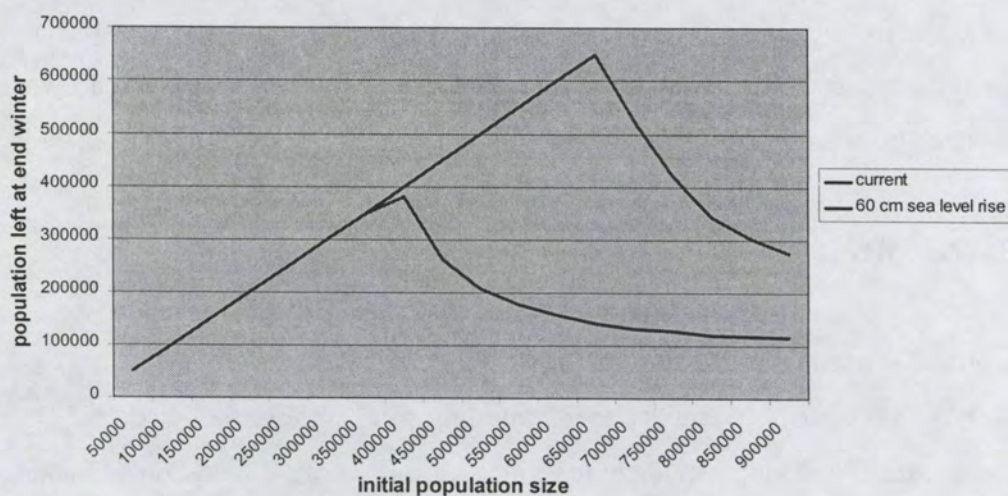


Figure 5.8: Results of simulations with DEPLETE for Oystercatchers using the Dutch Wadden Sea. The population predicted to survive the winter is plotted as a function of the initial population size for current conditions and when sea level would be 60 cm higher (average food supply and Beddington interference).

mass of 50 g (Fig. 5.7b), i.e. departure total masses of about 56 g, far lower than reality (70-85 g).

The general effects of habitat loss due to climate change

To study the effect of habitat loss due to climate change at migratory stopover sites, we used our dynamic optimization model. Since this is not an analytical model, our results suggest certain rules, but they cannot be taken as a definitive mathematical proof. Weber *et al.* (1999) discuss the results in detail. Here, we can only repeat the summary of their paper.

The model emphasizes costs birds face during stopover (e.g. costs of gaining energy), the timing of site use and the behavioural rules birds might use to implement migratory strategies. Behavioural rules may be flexible enough that birds can still produce optimal behaviour in the changed environment, or the rules may result in sub-optimal behaviour. If birds behave optimally in the altered environment, habitat loss on the wintering ground has the highest impact, because this site, unlike the intermediate stopover sites, cannot be skipped if the quality drops below a threshold. If birds continue to use the old behavioural rules that now result in sub-optimal behaviour, we can distinguish two cases. Birds can continue to use a constant foraging behaviour that was optimal in the unaltered environment under many circumstances. Then the effects of habitat loss are proportional to the length of stay before habitat loss and the departure fuel load from a site. However, the effects of habitat loss do not depend on the location of the site within the network.

In some circumstances birds are expected to forage with intensities that are below maximum. If birds use the foraging behaviour that is appropriate for a given fuel load, time and site but inappropriate for the altered fuel gain, then changes at sites close to the breeding ground have a greater impact than more distant sites. Finally we discuss the importance of sites that are not used before habitat loss. If birds behave optimally these sites may be used in an altered environment and can buffer against habitat loss at other sites.

5.3.2 DEplete

There are very few species on which we have sufficient data to calibrate DEplete. The Oystercatchers feeding on bivalves on the intertidal mudflats in the Dutch Wadden Sea are a notable exception. In the methods section we describe how we estimated the various

parameters. Once the model was fully parametrized for a particular interference function, we varied the initial number of Oystercatchers and calculated the number of individuals that would survive the winter for a given food supply. The particular shape of the interference function had little effect on the general results. In each case the number surviving equalled the initial number until a threshold value was reached, after which the number surviving decreased with increasing initial numbers. The threshold value can be interpreted as the carrying capacity for the particular food conditions of that year. When food conditions are average, slightly less than 700.000 Oystercatchers should be able to survive. This is far above the actual number observed, which varies between 200.000 and 250.000 in mild and normal winters (during cold winters large numbers of Oystercatchers leave the Wadden Sea). When food conditions are lower, the carrying capacity is also lower. This suggests that the number of wintering Oystercatchers is primarily determined during years of poor food supply. This makes sense, because shellfish stocks vary considerably from year to year, whereas Oystercatchers are long-lived birds with a low reproductive rate, so that their numbers vary only slowly. Their numbers will be hit badly during a poor food year and after such a hit numbers will increase only slowly until the next hit by a bad year.

It can now be investigated how sea level rise will affect this curve. When sea level rise is 60 cm and there occurs no compensation due to sedimentation, the maximum number of Oystercatchers is almost halved. This applies not only to years with an average food supply as depicted in Fig. 5.8, but also to years with a poor food supply. On the basis of the previous reasoning it seems therefore likely that the average number of Oystercatcher wintering in the Dutch Wadden Sea would decrease considerably as a result of such a drastic increase in sea level. Clearly, the next step is to link these results of DEplete with a model of the breeding season. That would lead to a version of LARGEPOP for Oystercatchers where the parameters have been estimated from individual-based models of competition during the breeding season and during the non-breeding season.

5.3.3 LARGEPOP

We did not find a significant density dependence in the survival of the Brent Geese during the non-reproductive season, i.e. in the statistical analysis the survival counts were found to be

directly proportional to the population size. In a log-linear model with only a constant and an offset for $\log(\text{population size})$, the constant represents the proportionality parameter. Let therefore

$$h(N_{2k}) = \delta \quad (5.37)$$

for all years, with δ the constant fraction of the population that does not survive the non-reproductive season (including death during the migration from Europe to Siberia). The estimate of δ over the 1955-1994 period equals 0.153 with 95% confidence interval (0.134 , 0.174). The years 1961 and 1986 were excluded from the analysis because they had negative death rates. We also tested whether survival differed in the period before and after the hunting ban in 1972. This resulted in the estimates $\delta = 0.182$ for the period 1955-1972 and $\delta = 0.149$ for the period 1973-1994. The two estimates were, however, not significantly different.

Next, we estimated the dependence of the number of first-winter birds on the total winter population size. In terms of the model, this amounted to plotting $Nf(N)$ as a function of N for different functions f . Only years in which the proportion of first-winter birds exceeded 15% were used in this analysis. This threshold value was chosen to exclude the years when successful breeding was impossible for other reasons like high predator levels on the breeding grounds or adverse headwinds during spring migration (Ebbinge 1989). We fitted several non-linear functions through the origin. The following functional form fitted the data best:

$$Nf(N) = (a + bN)Ne^{-cN} \quad (5.38)$$

where a, b, c are estimated as, with standard errors in parentheses: $a = 0.479$ (0.236), $b = 0.00001875$ (0.00000850), and $c = 0.00001199$ (0.00000209).

The model therefore becomes

$$\begin{aligned} N_{2k} &= N_{2k-1}(1 + (a + bN_{2k-1})e^{-cN_{2k-1}}) \\ N_{2k+1} &= N_{2k}(1 - \delta) \end{aligned} \quad (5.39)$$

with a, b, c regression parameters given above, and with the current per capita death rate $\delta = 0.149$. The model allows one or more steady states, depending on the value of δ . In Fig. 5.5 we summarised this behaviour in a bifurcation diagram, which gives the predicted value for the steady state at the start of the winter season (census date) as a function of δ , as δ is varied from 0 to 1. From this graph we can see that the current best estimate for δ would result in a

steady state population size of 300.000 birds. The model therefore predicts that the population is likely to stabilise at about 300.000 individuals at the start of the winter season.

From Fig. 5.5 we can also see that the model has a subcritical (i.e. backward) bifurcation as a function of δ . This has the following consequence: if we slowly increase δ from its present value, the steady state number of birds will gradually diminish. At some point, when $\delta = 0.44$ (approximately), the population collapses (even though for $\delta < 0.44$ it was still in the thousands) and the zero steady state is the only stable situation. When that has happened, one sees from Fig. 5.5 that decreasing δ will not have an immediate effect since there exists a steady state in between the stable zero state and the stable upper branch (this intermediate steady state is unstable and delineated by two dots in the graph). We have to decrease δ substantially, i.e. to below 0.32 (approximately) before we can regain a stable steady positive population. Biologically speaking our model therefore suggests that one has to be careful that δ is not increased significantly from its present value (e.g. due to renewed hunting to prevent agricultural damage for instance) because at some point the population might suddenly collapse completely, where after re-establishment is unlikely even if the unfavourable conditions are improved.

With this in mind we can also study the effects of habitat loss for migratory populations as in Fretwell (1972) and Sutherland (1996) based on intersections of curves representing the relation between population density and respectively mortality and reproduction. In the analysis presented in Sutherland (1996) only the steady state population density changes as a result of habitat loss. The reason for this is that the form of the two curves postulated is such that the dynamics of the corresponding system leads to a unique steady state. Of course, from a theoretical point of view, one can immediately state that the dynamics can become more complicated if the curves would behave differently so as to give rise to multiple steady states. What our analysis shows is that these more complicated situations can indeed occur in real systems, when the curves are estimated from data. This has as a consequence that the effects of habitat loss can be more dramatic than a gradual shift in expected steady state densities to adapt to new conditions.

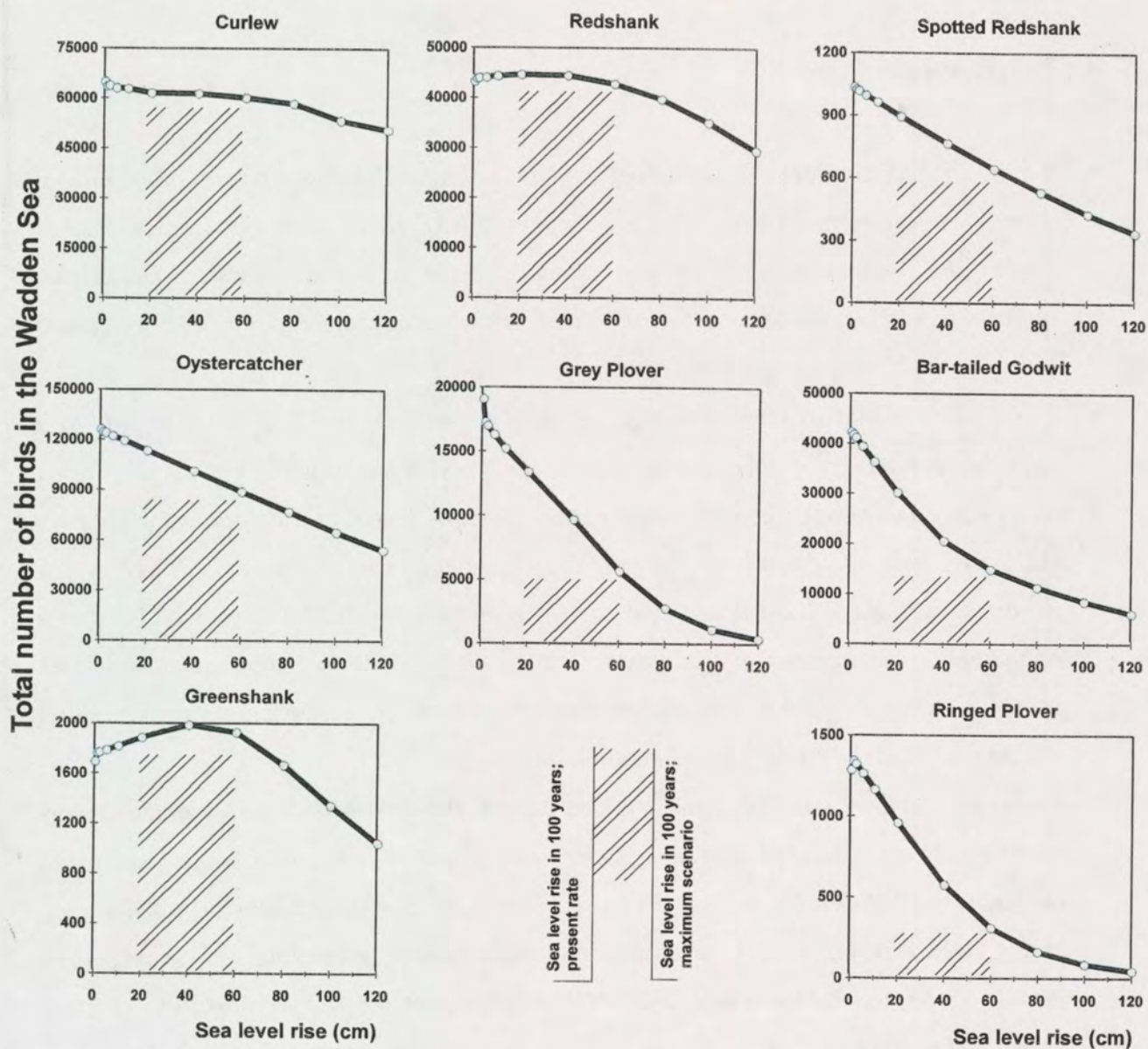


Fig. 5.9. Effect of sea level rise without compensation in the Dutch Wadden Sea on bird populations of selected species using the HABITAT model

5.3.4 HABITAT

When increased sea level rise is not compensated by sedimentation it will have a considerable negative effect on most of the waders feeding on the intertidal flats (Fig. 5.9). Greenshanks may profit at first, but when sea level rise exceeds 40 cm, this species will also start to decline like the other species. Especially grey plover, bar-tailed godwit and ringed plover are predicted to suffer from sea level rise.

5.4 Conclusions

- *A quite sophisticated set of interlocking models dealing with various phases of the annual cycle of migratory birds was developed as part of NRP II. These models can be used to predict the consequences of climate change for the migratory birds, provided that sufficiently precise scenarios are available of how climate change will affect the habitats on which the birds depend for their survival.*
- *Under many scenarios climate change will lead to sea level rise and this may lead to a reduction in the area of intertidal mudflats in the Wadden Sea, especially if the rate of sea level rise accelerates considerably above current levels. Calculations with both DEplete, which builds on knowledge of the underlying processes, and HABITAT, which is correlative, leave little doubt that such a reduction in mudflat area will lead to a reduction in the number of waders that can feed on those intertidal mudflats. More precisely, when the rate of sea level rise exceeds 60 cm per century, sedimentation will not keep up with the rising sea and mudflats will be lost.*
- *Excessive sea level rise may lead to a decrease in the area of salt marsh and this may affect the Brent Geese. A decrease in the area of salt marsh could either lead to an increased mortality rate, or to a decrease in the rate at which birds can fatten during spring, which would lead to a decrease in reproduction according to our migration models. In both circumstances LARGEPOP predicts that the world population of Brent Geese will decline.*
- *Climate change may also lead to a change in temperature and this will affect both the population dynamics of the invertebrate prey on which the waders feed and the timing of the growth of the salt marsh vegetation, which is important for the Brent Geese.*

- *During this study we focussed on the Wadden Sea. However, climate change will not affect this area in isolation, but will affect all areas used by the birds spending some part of their annual cycle in the Wadden Sea. The models that were built as part of this project are able to deal with these changes. What is needed as the next step are sufficiently precise scenarios of the combined effects of climate change on the wintering grounds, stopover sites and breeding grounds of well-studied migratory birds.*

6 EFFECTS OF CLIMATIC CHANGE ON BENTHIC FAUNA IN THE WADDEN SEA

6.1 Introduction

The aim of this project was to get insight into the flexibility of the benthic infaunal organisms from the Wadden Sea to changes in the environment due to global change. Only the effect of temperature is further investigated in this project, as it is believed to be by far the most important factor influencing the organisms of interest. As focal organism the common Baltic Tellin, *Macoma balthica* was chosen. *Macoma balthica* is a bivalve which lives buried in the sediment of the intertidal and shallow sub-tidal coastal areas. The European population ranges from the Gironde (France) in the south up to Nova Zembla in the north. This means that the Wadden Sea is a relative southerly habitat for this organism. From the commonly occurring shellfish in the Wadden Sea *Macoma balthica* is the species most adapted to low temperatures. This will be mainly due to its northerly distribution. Temperature changes can easily bring the circumstances close to the thermal limits within which *Macoma balthica* can survive.

The main question asked is "What is the flexibility of *Macoma balthica* to differences in the thermal environment". This question can be divided into several levels. First one can consider the range of temperatures in which an individual *Macoma balthica* from the present local population is able to flourish. This question can be subdivided into several more detailed questions:

- how do the important life history variables growth reproduction and survival depend on temperature
- how well can the individual respond to novel situations.

The second level is the population which is build up by the individuals. They will vary in their ability of coping with higher temperatures. This question can be rephrased as:

- How much of this variation is plasticity of the phenotype and how much is genetic? That information is important to predict the response of the population to the new selective environment.

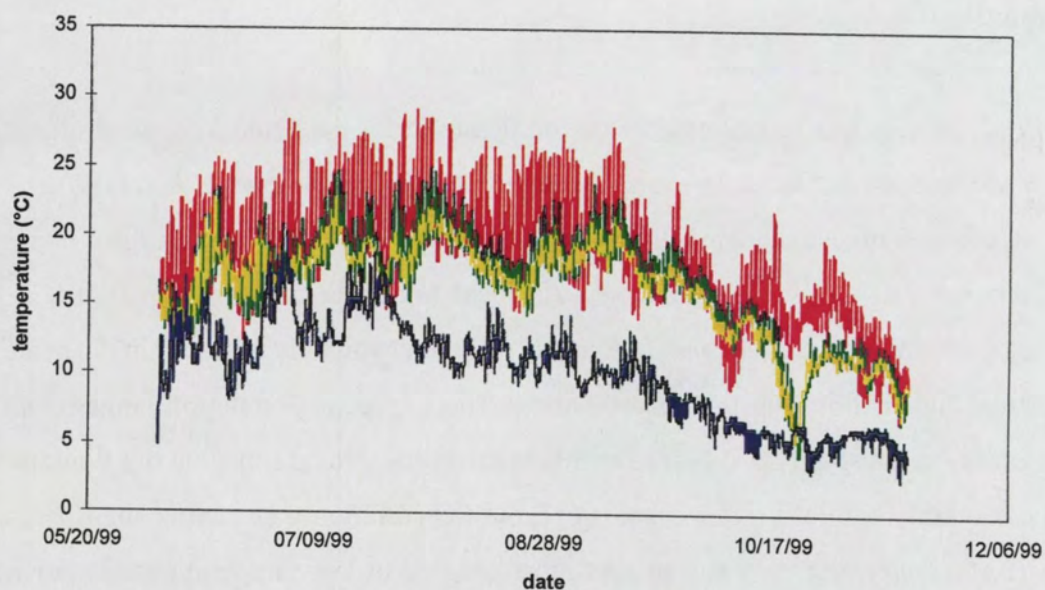


Fig. 6.1 Temperature of the sediment at a depth of 5 cm. The upper red line is from the Gironde. The yellow and green line are from the Mokbaai and Balgzand respectively, both in the Wadden Sea. The lower line blue represents the sediment temperature in Balsfjord.

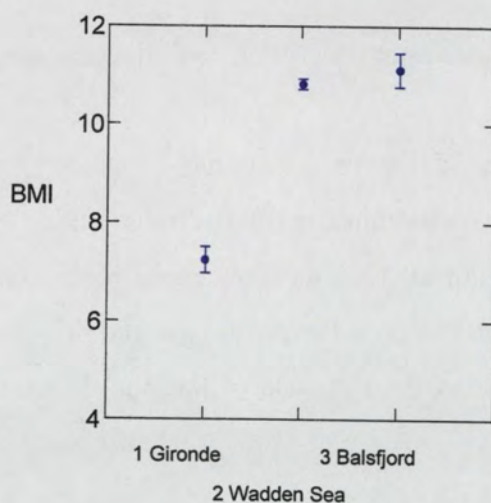


Fig. 6.2 Comparison of the mean body mass index from Gironde, Wadden Sea and Balsfjord.

Thirdly there are questions on the meta-population level. This consists of the total of *Macoma balthica* in Europe. Matter of interest here is the magnitude of structuring.

- Is everything just one gigantic mixing pool of all genetically identical *Macoma balthica* or do the different habitats throughout the distribution range have their own genetically distinct populations adapted to the local circumstances? This can shed light on the question what will be the final result if the local population doesn't make it. Is it possible that populations from elsewhere (from warmer areas further south) replace the present local population?

In order to get answers to the above raised questions, both field- and experimental-studies were carried out.

6.2 Study areas and methods

Two latitudinal different sites were selected to compare *Macoma balthica* populations from the Wadden Sea with populations occurring in naturally different thermal habitats. In the south, the mouth of the Gironde in France at the limit of the distribution of *Macoma balthica* was chosen. In the north the colder Balsfjord in Norway was selected. To quantify the thermal environment the intertidal *Macoma balthica* population experiences, data loggers were buried 5 cm deep in the sediment, recording temperatures at an interval of twenty minutes measures. These measurements have been synchronously collected in the Balsfjord, Wadden Sea and Gironde from June until November 1999 (Fig. 6.1).

Mean body mass indexes were studied by collecting *Macoma balthica* in the Wadden Sea and the Gironde in 1979. Balsfjord samples were collected in 1999 and 2000. From all collected animals the shell size has been measured, their age has been estimated by counting the growth rings of the shell. The soft parts of the individual shellfish were dissected into somatic tissue and gonadal tissue and dried at 60°C for at least 3 days. The dried samples were weighed and ashed at 560°C and weighed again to determine the ash free dry mass.

The general practical set-up and methods on MOTIF-experiments can be found in Kersting (this volume, Chapter 5). Of each of the four (two warm and two cold) experimental groups 18 specimens were taken from the samples of December 1998 and January 1999. Each animal was fresh dissected in two parts, somatic tissue and gonadal tissue. The samples were dried at 60°C

and ashed at 560°C in order to determine ash free dry mass AFDM. Measures, body mass index (BMI) divided in somatic mass index (SMI) and gonad mass index (GMI) are all expressed as mass (mg) per cubic shell length (cm³) to be able to compare animals with different shell length. Egg-sizes were measured in March, individuals were placed separately in jars and induced to spawn by applying a temperature shock and a solution of PROZAC (Honkoop et al. 1999). Eggs were collected, photographed and diameters measured on slide. In the analyses means of the experimental groups were used. A linear backward stepwise model was used to describe the data of BMI, GMI and SMI.

Settlement experiment of larvae of *Macoma balthica* have been carried out using adults from the Gironde (France) and the Balsfjord (Norway). After being collected they were transported to the laboratory where adults were individually induced to spawn by applying PROZAC and a temperature shock (Honkoop et al. 1999). From each origin four crosses were formed. Each cross was transferred to two litres of filtered sea water with antibiotics added, for three days at 15°C. After three days the larvae from each pair were split into three batches. From each pair the three groups were placed at 10°C, 15°C and 20°C and supplied with *Isochrysis galbana* as food source and antibiotics. After 15 days every two days a sub-sample of the larvae was measured and the development of the foot was scored. The appearance of the foot is an indication that the larvae are ready to settle.

Table 6.1 Sediment temperature at a depth of 5 cm, recorded every 20 minutes. At four sites, Gironde (France), Balgzand & Mokbaai (Wadden Sea) and Balsfjord (Norway). Measurements were taken from June 1999 until October 1999.

	mean	minimum	maximum	range	variance	standard deviation
Gironde	18.6	6.9	29.2	22.3	15.3	3.9
Balgzand	16.6	4.2	24.9	20.7	14.1	3.8
Mokbaai	16.2	5.4	22.8	17.4	12.4	3.5
Balsfjord	10.2	2.5	20.2	17.7	11.6	3.4

6.3 Results

Results have been summarized in Table 6.1. Mean temperatures as well as the maximum and variances are relatively high in the Gironde. The mean temperatures in the Balsfjord are the lowest and least variable. The Wadden Sea has an intermediate position but shows a higher resemblance with the Gironde, with only 2°C lower mean temperatures. The difference with the Balsfjord is about 6°C. The two locations at which temperatures have been recorded in the Wadden Sea show comparable results, indicating that within the geographic locations variation is small as compared to the variation between locations. For *Macoma balthica* in the Gironde not only the mean temperature is highest but also the fluctuations the largest. In the short term temperatures fluctuate with an amplitude of more than 10 °C. For the rates of physiological processes this means that they will change with at least a factor two (Q_{10} of 2). Macrobenthic animals in this area have to cope with a broad spectrum of temperatures.

Mean body mass index (BMI)

An important issue is try to understand which factors are determining the range of occurrence in *Macoma balthica*. Why does it not occur further south? Are the environmental conditions, biological or physical, that far from optimal that the species has trouble to survive and reproduce? In the context of this study especially the effects of the physical environment on the functioning of *Macoma balthica* are of interest. A possible way to get an idea is to quantify some important life history parameters, survival, growth and reproduction at different places in the distribution range.

Mean body mass index (BMI, ash free dry mass per cubic shell length, $\text{mg}\cdot\text{cm}^{-3}$) for *Macoma balthica* at the three focal sites are lowest in the Gironde (Fig. 6.2). The Wadden Sea and Balsfjord give similar results. The mean gonadal body mass index (GMI, ash free dry mass of the gonadal tissue per cubic shell length, $\text{mg}\cdot\text{cm}^{-3}$) in spring is also lowest at the southern limit of the distribution of *Macoma balthica*, the Gironde. Again Wadden Sea and Balsfjord have similar values (Fig. 6.3). The growth parameters k and l_{max} , estimated using the Von Bertalanfy growth equation, do not show latitudinal patterns.

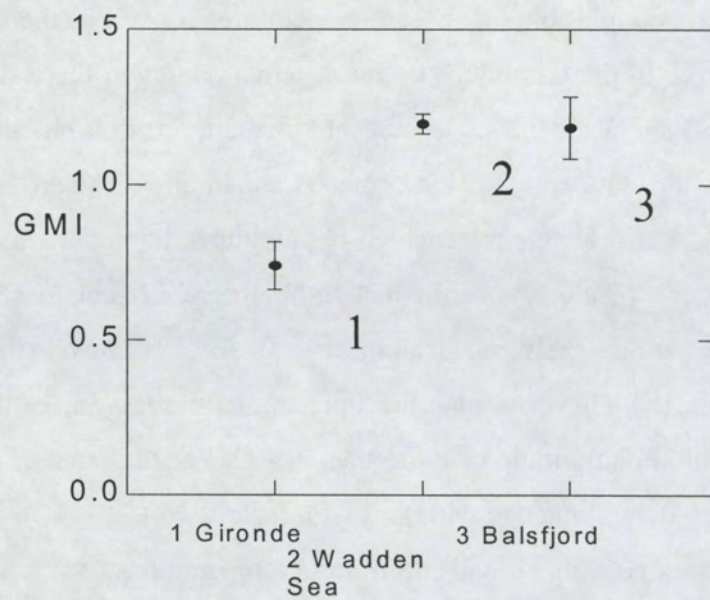


Fig. 6.3 Comparison of the mean gonal mass index ($\text{mg} \cdot \text{cm}^{-3}$) from Gironde, Wadden Sea and Balsfjord in spring

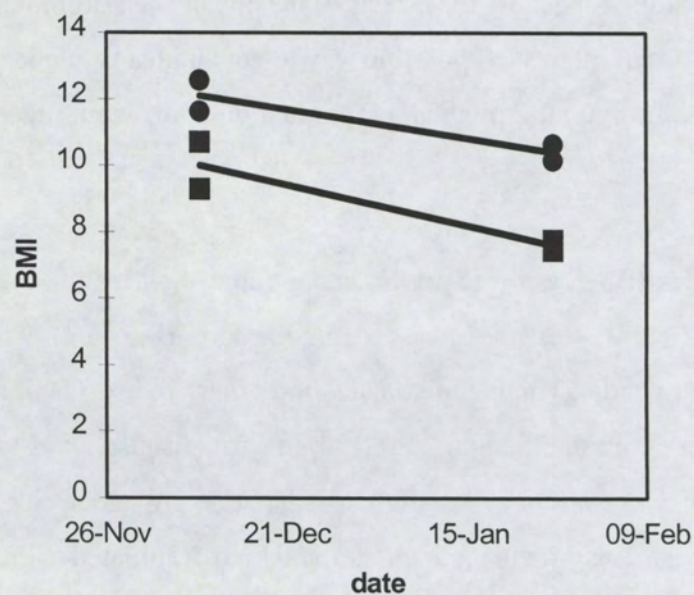


Fig. 6.4 BMI in the motif experiment. The circles and squares represent the cold and warm treatment respectively

The results are consistent with the idea that *Macoma balthica* is more constrained at the border of its distribution. The body condition is lower as well as the reproductive output, quantified by gonadal mass. A second reproductive period in the autumn besides the one in spring mentioned for the Gironde (Bachelet 1980; Bachelet 1986), was not found in this study.

Experiments using MOTIF's

The effect of elevated temperatures on the benthic community was studied in model tidal flat ecosystems, as has been described by Kersting (c.f. Chapter 7). Within this experiment specific attention was paid to the reproduction of *Macoma balthica*. Long term field observations showed that after cold winters recruitment of *Macoma balthica* generally was good after cold winters (Beukema et al. 1998). In a later study winter temperatures have been manipulated, resulting in larger egg numbers produced by the females after cold winters compared to warm winters (Honkoop and Van der Meer 1998). The results were explained by considering the energetics during winter. During winter the food conditions are poor, so for the energetic needs the animal must depend on the reserves build up in the past. The amount of energy needed just for maintaining the body is dependent on temperatures, the higher the temperature the higher the maintenance energy. During warm winters more energy will be consumed for maintenance so less will remain for eggs, resulting in a lower egg production. As a mechanism it was proposed that the actual energy reserves are made up by the eggs. The eggs are synthesised before the winter and partly resorbed during winter to meet the energy demands to survive (Honkoop and Van der Meer 1998).

Egg size is another important parameter in reproduction that also received attention. Experimentally changed winter temperatures did not have an effect on egg size (Honkoop and Van der Meer 1998) although field studies showed marked differences between sites. These differences were correlated with the BMI in August.

Two hypotheses resulting from the study by Hopkoop & Van der Meer have been tested in the MOTIF temperature experiment. The first one is:

- Eggs are synthesised before winter and are being used as energy reserves by resorbing eggs during winter. The second:
- Egg-size is determined by BMI in autumn when the eggs are synthesised.

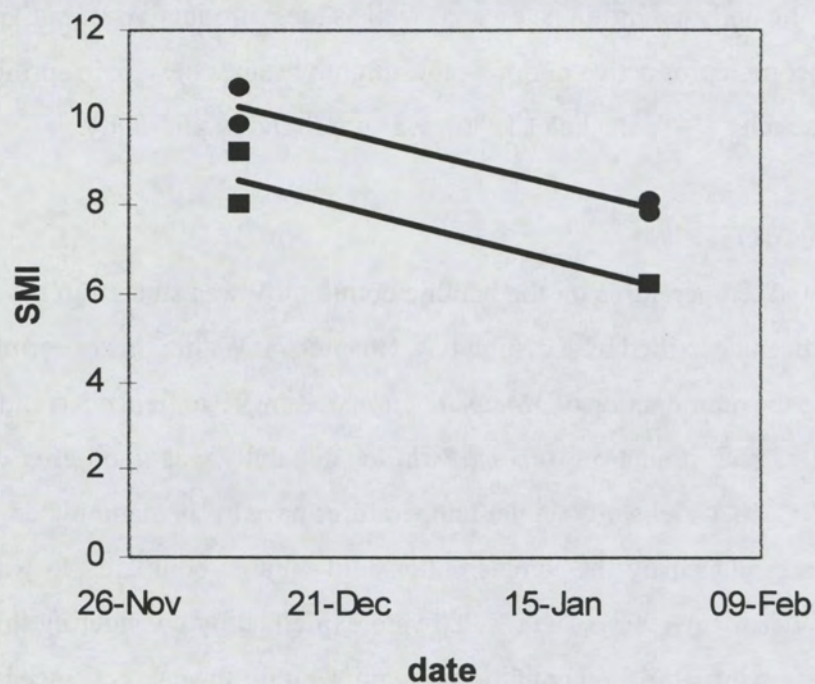


Fig. 6.5 Somatic mass index ($\text{mg} \cdot \text{cm}^{-3}$) in the motif experiment. Circles stand for the cold treatment, squares for the warm treatment.

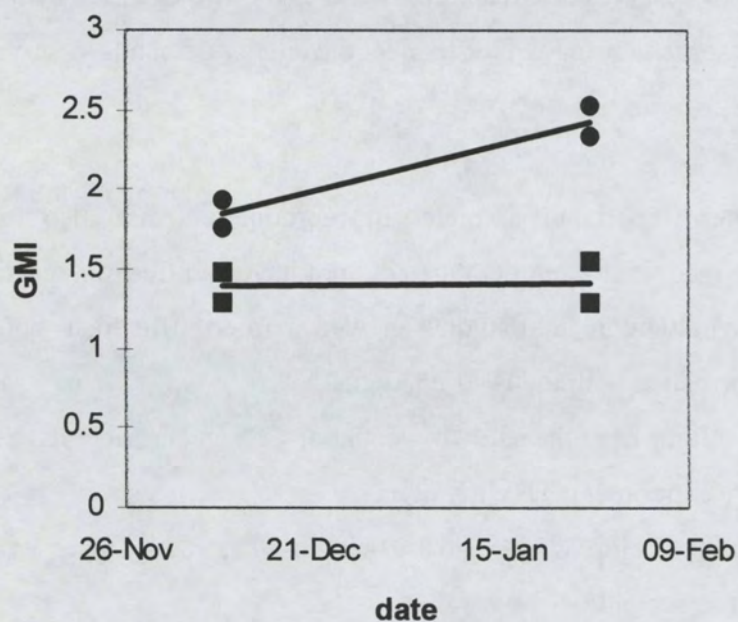


Fig. 6.6 The development of the gonadal mass index ($\text{mg} \cdot \text{cm}^{-3}$) in the MOTIF experiment. Circles represent the cold treatment, squares the warm treatment.

This last experiment differs from previous ones in that the temperature manipulation is started in spring generating differences in BMI in summer, well before the moment of proposed egg-size determination. Earlier manipulation experiments started before or in October, generating differences in BMI in December, and no egg-size differences.

Fig. 6.4 shows the development of the BMI during winter. The level in the warm treatment is significantly lower than in the cold treatment, the decrease in BMI is the same for both treatments. When viewing the two components in which the BMI is split up the same pattern emerges for the SMI as for the BMI (Fig. 6.5). The cold treatment has a higher SMI than the warm treatment, whereas the decrease in SMI is similar. The gonadal index yields another picture (Fig. 6.6). The warm treatment shows no development of gonadal mass at all whereas in the cold treatment animals increase their gonadal tissue. The intercept is not statistically distinguishable whereas the interaction term is significant.

Egg-size variation does not show any relation with treatment. In a nested analysis most variation could be attributed to female, the only significant factor (Table 6.2). The highest egg production expressed as gonadal mass was found in the cold treatment. This result was to be expected as could be inferred from earlier observations. The proposed mechanism, however, does not match the results. In the beginning of the winter the GMI in both treatments is the same. Only during the winter things start to change. In the warm group the GMI remains the same whereas in the cold group the GMI increases.

Table 9.2 Results of a nested analysis of egg size variation in a model tidal flat system. A temperature treatment consisted of two levels with a difference of 4°C.

	df	ss	ms	F	p
treatment	1	210.8	210.8	7.18	>0.05
group	2	58.74	29.37	0.1	>0.05
motif	4	1171	292.8	1.21	>0.05
female	29	6998	241.3	17.3	<0.001
error	458	6389	13.95		

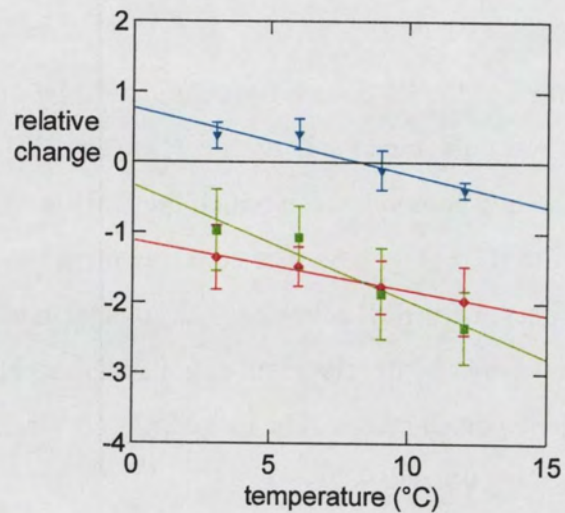


Fig. 6.7 Development of the gonadal mass (triangles), somatic mass (diamonds) and total body mass (squares) of *Macoma balthica* as a function of temperature while starved.

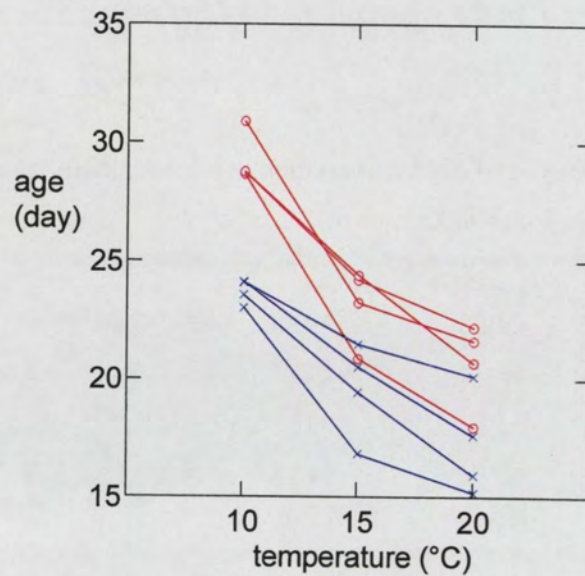


Fig. 6.8 Age when 50% of the larvae has developed a foot as a function of temperature. Larvae from Balsfjord are shown with a circle, larvae from Gironde with a cross

BMI levels were different but not the changes in BMI. This is contrary to earlier results of Honkoop & Beukema (1997) who found that the decrease in BMI is strongest in warm winters as compared to cold winters. The statistical power of this experimental set-up, however, is very limited. There was no effect of treatment found on egg-size, neither directly due to different temperatures of the environment nor indirect by BMI differences induced by temperature. The relationship between BMI in August and the egg-size in March of the following year, found in the field by Honkoop and Van der Meer (1998), is hard to understand. Eggs must be tuned to the environment in which they have to develop. This is the same for the groups between which this relationship was found by Honkoop & Van der Meer (1998). The BMI of the parent should not have anything to do with the optimal egg-size. That will only influence the egg number. Direct differences in the environment like temperature could cause a shift in the optimal egg-size and are much more probable. This response of egg-size is not found in the present study.

The final conclusion from this experiment is that the reproductive output depends on the BMI or the amount of reserves and the rate in which the reserves are being used for other processes than the production of eggs or sperm. Egg-size is not influenced by the BMI of the adult animal. The hypothesis that temperature acts as an environmental cue for the determination of egg-size does not get any support in this experiment.

The effect of temperature on gonadal development

Results of the above mentioned MOTIF experiment concerning the developments in body mass index (BMI), somatic mass index (SMI) and gonad mass index (GMI) were confirmed and elaborated on in another separate experiment. From January to April *Macoma balthica* were kept without food at four different temperatures. Four samples were taken through time. Somatic and gonadal tissue were separated and dry weights determined.

The development of total body mass, somatic body mass and gonadal body mass are plotted in Fig. 6.7. In all treatments the total body mass declines, the decline increases with temperature. The same is true for somatic body mass. The gonadal mass however increases in the lowest temperatures. At 9°C it remains constant, while at 12°C gonadal mass decreases in the same way as somatic mass.

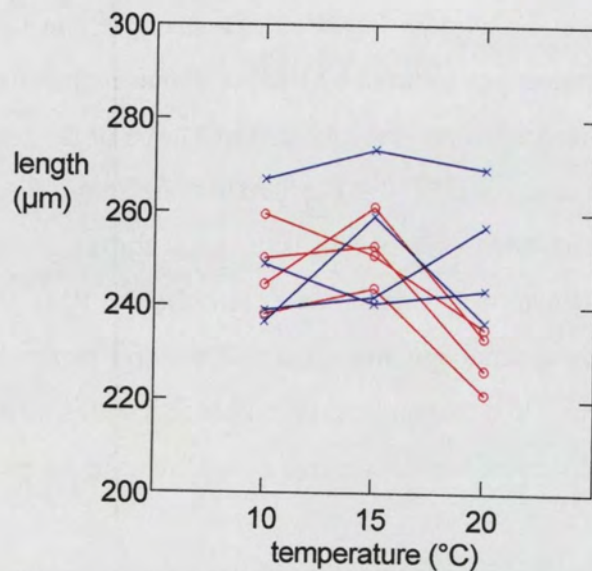


Fig. 6.9 Length at which 50% of the larvae from the Balsfjord (circles) and the Gironde (crosses) have developed a foot at three different temperatures.

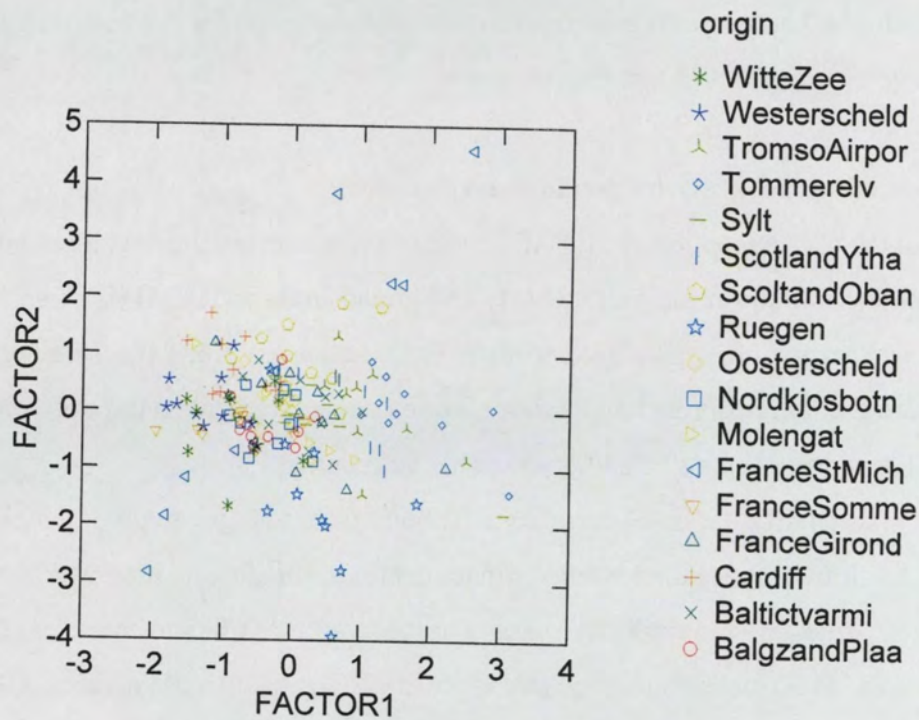


Fig. 6.10 Plot of factor 2 against factor 1 of a principal component analysis on 14 shell morphological characters from the European *Macoma balthica*

A decline of total body-mass is to be expected since no energy intake was possible. Reserves were used to survive. Under very low temperatures energy reserves are not only allocated towards maintenance processes but also to reproduction. At the highest temperature of 12°C not only the somatic mass is declining but also the gonadal mass. Energy which has first been allocated towards reproduction is redirected towards maintenance processes. This is an inefficient process. The conversion of energy into reproductive tissue will cause losses as the conversion back to a metabolizable form will induce losses to. The mechanism proposed by Honkoop & Van der Meer (1998) is therefore energetically inefficient and will only be used as a rescue system in extreme conditions. Under normal conditions during winter energy reserves are allocated to maintenance processes and reproduction. The net amount of energy finally converted in eggs or sperm at the moment of spawning in spring is dependent on temperature in the preceeding winter.

The results show that when starving, *Macoma balthica* gonadal build-up will continue only under lower temperatures. At higher temperatures maintenance processes require all available energy. Field data show that the same processes operate in the wild as well.

Larval development: the effect of temperature and latitude.

In the first few weeks of their life *Macoma balthica* develop as planktonic larvae, before settling in the sediment. This is a crucial phase in the life history of *Macoma balthica* with high mortality rates. The larval phase is very important for the population dynamics. Once settled the mortality rates are more or less constant, the success of a year class is highly dependent on the pelagic phase (Van der Meer, 2001). Because settlement is such a risky part of life it can be expected that there is heavy selection pressure to reduce this dangerous period. This hypothesis was tested by experimentally comparing the development of Balsfjord and Gironde larvae under different temperatures.

The time at which 50% of the larvae had a foot was determined for each batch by fitting a logistic curve for the relationship between developmental stage and age. The results are plotted in Fig. 6.8. Under all temperatures the Balsfjord-group shows the slowest development of foot, taking approximately 5 days than the Gironde-group. In both groups elevated temperatures have a strong reducing effect on the development- time. There is no significant origing*temperature interaction.

The length of the shell with developing feet was also determined by fitting a logistic curve for the developmental stage-length relationship. The results (Fig. 6.9) show that origin alone does not have a significant effect on the size at metamorphosis. The origin*temperature interaction is significant. The factor temperature also significantly explains part of the variation.

Obviously the larvae from two different origins do not behave in the same way. The Gironde-group develops faster under all temperature treatments. At the same time the size at metamorphosis is similar or even larger in the Gironde-group, which means that they grow faster than the Balsfjord-larvae under further identical conditions. In some way or another the Gironde-larvae must be more efficient in converting the available food into growth. This could be the result of a higher food intake rate. At 20°C, a temperature never to be encountered in the Balsfjord, the smaller size at metamorphosis in the Balsfjord-larvae may indicate that this temperature acts as a stress-factor. In the other cases the size at metamorphosis is approximately the same. The results indicate that Gironde-larvae are better adapted to high developmental temperatures.

Shell morphology from different sites.

Beukema & Meehan (1985) observed latitudinal trends in a number of shell characteristics of *Macoma balthica*. In mussels as well as in oysters differences in shell characteristics make it possible to distinguish between species which are in first sight alike (McDonald, Seed et al. 1991; Day et al. 2000). If differences between species can be shown, patterns of population structuring within a species also might be visible in variations in shell morphology. From a large number of different sites in Europe samples of *Macoma balthica* were obtained. From twelve shells from each site fourteen different measures were taken. Dimensions and shape of the shell, muscle scars, pallial line, hinge and ligament were included. In a principal component analysis the data were reduced to three principal factors. Fig. 6.10 shows a plot of factor 1 against factor 2. No clear separations of geographic groups become clear. All groups are overlapping somehow. For all three factors the site of origin has a significant effect for the loadings, as tested by ANOVA.

There is a lot of site-specific variation in the shell morphology of *Macoma balthica*. At least part of the morphological differences have a genetic basis, as has been shown in laboratory breeding experiments (Luttikhuisen et al. in prep). There is no relationship with the resemblance in

morphology and distance between the sites. Such a relationship might be expected, since populations living close together would have more gene flow than more distant populations.

Concluding, shell morphology does not envision a clear geographic structuring, at least not at the scale investigated in the present study. Possibly on a smaller scale patterns will emerge with habitat type as the explaining variable rather than distance.

6.4. General conclusion

Macoma balthica in the Gironde at the southern border of its distribution have a lower Body and Gonadal Mass Index, and a lower larvae growth development than living populations further north. This can be the effect of higher environmental temperatures, which is clearly demonstrated through experimental work. There is some evidence that there are differences in *Macoma balthica* between sites. Shell morphological studies show large differences but no clear pattern. Development of larvae from the Gironde are not affected at high temperatures like the Balsfjord larvae are. The results indicate that European population(s) of *Macoma balthica* will for sure be affected by higher temperatures. Populations now living further south are possibly better adapted to higher temperatures. Considering the dispersal abilities of *Macoma balthica* these populations might have a chance to move northwards when situations change.

